THE AMPHIPOD GENUS *ALLORCHESTES* IN THE NORTH PACIFIC REGION: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

By E. A. Hendrycks[1] and E. L. Bousfield [2]

Abstract

The talitroidean amphipod family Hyalellidae Bulycheva 1957, emend Bousfield, 1996, and herewith redefined, encompasses the marine genera *Allorchestes* Dana, *Parhyalella* Kunkel, *Exhyalella* Stebbing, *Marinohyalella* Lazo-Wasem & Gable, and the neotropical freshwater genus *Hyalella* Saussure. From the Pacific coast of North America are newly described and figured ***Allorchestes rickeri*** n. sp. (S.E. Alaska to Central California) and ***A. priceae*** n. sp. (S.E. Alaska to southern Vancouver Island). Character states of reproductive morphology are newly utilized in redescribing and refiguring *Allorchestes angusta,* Dana (Alaska to California), *A. bellabella* Barnard (Kamchatka and Bering sea to Oregon), *A. carinata* Iwasa (Northern Sea of Japan, Bering Sea and S.E. Alaska), *A. malleola* Stebbing (northern Sea of Japan and Okhotsk Sea), *A. hirsuta* Ishimaru (southern Sea of Japan), and undescribed species of *Parhyalella* and *Hyalella.* Numerical analysis of selected characters and character states, partly developed recently by Lazo-Wasem & Gable, supports taxonomic recognition of family Hyalellidae and its distinction from the closely related marine family Hyalidae, and indicates degrees of morphological similarity and probable closeness of relationship between and among its five recognized genera. Species of *Allorchestes* dominate littoral marine habitats of boreal and cool-temperate open and semi-protected sand bottoms having submerged algal and phytal mats. Species of *Hyalella* occur in tidal freshwater portions ofestuaries and in coastal freshwater lakes and ponds of western North America, from Alaska to Southern California.

INTRODUCTION

The talitroidean genus *Allorchestes* was first proposed by Dana (1849), based on species shortly afterwards described as *A. compressa* Dana 1853, and *A. novizealandiae* Dana, 1853, from the Australian-New Zealand region of the South Pacific. Member species do share with member species of talitroidean family Orchestiidae (now Talitridae) some apomorphic character states such as maxilla 1 palp minute or lacking, and telson entire or apically cleft. However, the name "*Allorchestes*" ("other orchestes") is somewhat of a misnomer since member species are mainly aquatic and apparently non-saltatory, not terrestrial or semiterrestrial or capable of jumping actively in the air .

In the North Pacific region, *Allorchestes angusta* was described from the coast of California by Dana (1856), reaffirmed by Stimpson (1857), and subsequently found to be the common species of the entire region (below). In 1854-55, Stimpson described *Allorchestes rubricornis*, *A. penicillatus*, and *A. japonicus* from coastal waters of Japan. Despite the inadequate descriptions and lack of figures, these species continued to be listed in Bate (1862) and even in the recent catalogue of Ishimaru (1994). Character states of the eyes of *A. japonicus* suggested a species of *Hyale* similar to *H. pontica* (see Della Valle 1893), but was later transferred to the synonymy of *A. compressa* Dana by Barnard & Karaman (1991). *Allorchestes seminuda* described by Stimpson (1857) from the Central California coast, has not been recognized subsequently and may be synonymous with *A. angusta* Dana. Stebbing (1899,1906) described in detail *A. malleolus* from seaweed in the Yellow Sea and Sea of Japan. During the twentieth century, three further western Pacific species were described: *A. vladimiri* Derzhavin, 1937 from the Sea of Okhotsk, *A. carinata* Iwasa, 1939 from Okhotsk Sea and Sea of Japan, and *A. hirsuta* Ishimaru, 1995, from the Sea of Japan. Tzvetkova (1990) extended the ranges of *A. carinata* and *A. bellabella* to the Kamchatka peninsular region. Previous records from the Japanese region were summarized by Ishimaru (1994).

Along the North American Pacific coast, Stout (1913) described, but did not illustrate, *Allorchestes oculatus* from the Laguna Beach region of S. Californnia, a species later synonymized with *A. angusta* Dana. Significant contributions to the systematics of regional species of *Allorchestes* were made by Barnard, including redescriptions of *A. angusta* (1952, 1954, 1970, 1979), *A. carinata* (1979), and a formal new description of *A. bellabella* (1974, 1979, first figured in 1954). North Pacific species, including those of Hawaii (Barnard 1970), were compiled by Barnard & Karaman (1991), and those of North America by Bousfield (2001) .

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In a preliminary report on species of family Hyalidae in the North American Pacific region, Bousfield (1981) included eight species of *Allorchestes,* These and earlier records of *A. angusta* and *A. bellabella* Barnard 1974 were summarized by Ricketts & Calvin (1968), Barnard (1975), Austin (1985) and Staude (1987).

Based mainly on the results of regional field expeditions of the National Museum of Natural Sciences (now the Canadian Museum of Nature), the present study extends knowledge of the systematics and distributional ecology of the genus *Allorchestes* and other members of family Hyalellidae on the Pacific coast of North America.

ACKNOWLEDGMENTS

For assistance with field work the authors are greatly indebted to regional marine laboratories, notably the Pacific Biological Station, Nanaimo, B. C., the Pacific Environmental Institute, West Vancouver, B. C., the Bamfield Marine Station, B. C., and the Friday Harbor Laboratories, WA. Much of the detail has been acknowledged in previous station lists (below). Dr. Craig P. Staude, Dr. Colin B. Levings, the late Dr. Josephine F. L. Hart, and the late Dr. Daniel B. Quayle were especially helpful with the field collecting.

The authors are grateful to Drs. Peter Slattery and Charles E. O'Clair for providing valuable study material from the Bering Sea and Aleutian Islands regions. Dr. Nina Tzvetkova, Zoological Museum, St. Petersburg, provided helpful commentary and loan of valuable western North Pacific material. We much value the careful research of Dr. Shin-ishi Ishimaru on *Allorchestes hirsuta* in Japanese coastal waters, and for his kind permission to reproduce his published figures of that species (1995) as deemed essential to the cohesion of this study.

Taxonomic work on CMN amphipod collections was performed initially by ELB as a staff member of the National Museum of Natural Sciences at the Holly Lane Laboratory, Ottawa, during the period 1979-1984. Original line illustrations were prepared with the capable assistance of artist Floy E. Zittin, Cupertino, California. Marjorie Bousfield provided translations of the Russian literature.

The work was carred out mainly in the research laboratories of the Canadian Museum of Nature. The authors are especially grateful to assistant collections manager Judith C. Price for help in retrieving, cataloguing, and labeling of CMN amphipod material.

MATERIALS AND METHODS.

Station lists pertinent to field material utilized in this study are provided in Bousfield (1958, 1963, 1968); Bousfield & McAllister (1962); and Bousfield & Jarrett (1981),

The following abbreviations are used in the text and figures:

A1-2	-	antenna 1, 2
BR	-	brood lamella
CLSP	-	clothespin spine
CX	-	coxal plate
DACT	-	dactyl
EP	-	abdominal side plate
GN1-2	-	gnathopod 1, 2
HD	-	head
LFT	-	left
LL	-	lower lip (labium)
MD	-	mandible
MX1-2	-	maxilla 1. 2
MXPD	-	maxilliped
P3-7	-	peraeopods 3, 4, 5, 6, 7
PL	-	pleopod
PLP	-	palp
RET	-	retinacula
RT	-	right
SP	-	spine
T	-	telson
U	-	uropod
UL	-	upper lip (labrum)
UROS	-	urosome
X	-	enlarged
im	-	immature
juv	-	juvenile
ov	-	ovigerous
subad.	-	subadult

SYSTEMATICS

Family Hyalellidae Bulycheva

Hyalellidae Bulycheva, 1957: 18. Bousfield 1982: 270; 1996: 176.

Talitridae (part) Stebbing 1906: 523. Gurjanova 1951.

Hyalidae (part) (subfamily) Barnard 1970: 268. Bousfield 1981: 176.

Talitroidea (part) Barnard & Barnard 1983: 161.

Type genus *Hyalella* Smith, 1874.

Genera: *Allorchestes* Dana, 1849: 136; *Exhyalella* Stebbing, 1917, revised Lazo-Wasem & Gable 2001: 51; *Marinohyalella* Lazo-Wasem & Gable, 2001: 67; *Parhyalella* Kunkel, 1910: 74. Laso-Wasem & Gable (2001) have recommended suppression of the enigmatic genus *Insula* Kunkel, 1910, and we herewith concur.

Diagnosis: Body smooth, occasionally carinate or processiferous, mainly abdominally. Antennae relatively short. Antenna 2 longer than antenna 1, peduncle (male) occasionally stout and proximal flagellar segments conjoint (incrassate).

Mouthparts of generalized talitroidean form. Mandible, left lacinia 5-6 dentate; blades of spine row few (2-4); molar seta tending to reduction or loss. Maxilla 1, palp minute or lacking. Maxilla 2, inner plate with 1-2 prominent inner marginal setae. Maxilliped, outer plate short; palp moderate, dactyl unguiform.

Coxal plates 1-4 deep, subrectangular, posterior marginal cusp (acclivity of Barnard 1979) vestigial or indistinct. Gnathopods usually strongly sexually dimorphic. Gnathopod 1 (male), often modified for preamplexus; dactyl and propodal spines modified for fitting into precopulatory notch of peraeon 2 of female. Gnathopod 2 (male) powerfully subchelate; propodal palm smoothly convex or weakly toothed; carpal lobe well developed, interior margin lined with comb setae.

Peraeopods 3 - 4 slender, distal segments posteriorly armed with singly inserted complex spines; dactyls simple. Peraeopods 5-7, bases broad, hind margin lacking "surge seta" and corresponding indentation; distal segments typically slender and weakly spinose; dactyls small to medium, lacking median seta or locking spine; basis of peraeopod 7, posterodistal lobe lying mediad of ischium.

Epimeral side plates ordinary, plate 2 deepest. Pleopods normal, rami not sexually dimorphic; peduncle with 2-3 small retinacula; inner ramus proximally with claviform "clothespin" spines. Uropods 1 - 2 short, peduncular distolateral and/or distomedial spines ordinary; rami variously (or not) marginally spinose, apical spines occasionally striate. Uropod 3 uniramous; ramus distinct, short, not fused to peduncle. Telson plate-like; lobes fused basally, separated by distal notch only, or fused totally.

Coxal gills medium, sac-like, subequal. Sternal gills (when present) paired, sublinear.

Female: Peraeon segment 2 with anterodistal preamplexing (precopulatory) notch (Figs 1B, 6). Brood plates large, subrectangular or ovate and distally acute; marginal hooked setae short to medium in length.

Distributional Ecology: Within the North Pacific marine region, species of the genus *Allorchestes* are largely endemic to cool-temperate waters of both eastern and western coasts. The tropical and warm-temperate genus *Parhyalella* is represented in Taiwan by *P. kunkeli* Lazo-Wasem & Gable and in the southern Japan Sea by an undescribed species; in the Hawaiian Islands by *P. pietschmanni* Schellenberg; and on the Pacific coast of North America (Baja California) by *P. barnardi* Lazo-Wasem & Gable. Species of *Hyalella* occur in coastal fresh waters of North America north approximately to the tree line in Alaska.

Remarks: Not all systematists (e.g., Barnard & Karaman 1991; Lazo-Wasem & Gable 2001) accept the original concept of family Hyalellidae and generic inclusions that were split off from family Hyalidae by Bulycheva (1957). Barnard (1969) subsequently created Chiltoniinae, within the Ceinidae, to encompass the antipodean freshwater genera *Chiltonia, Austrochiltonia,* and *Afrochiltonia.* The aberrant hyalid genus *Hyachelia* Barnard (1967: 120), tentatively placed within the talitroidean family Najnidae by Bousfield (1982), was also placed within Ceinidae by Barnard & Karaman (1991). However, its true family status remains enigmatic.

Subfamily Chiltoniinae Barnard 1969: 467 (part). is herewith removed from the Hyalellidae. Its genera, along with marine genera *Allorchestes* and *Parhyalella,* had been placed within family Hyalellidae by Bousfield (1982, 1996). Chiltoniin genera lack: (1) a carpal lobe in male gnathopod 2; (2) a precopulatory notch in peraeon 2 (female); and (3) a corresponding modification of the propod and dactyl of gnathopod 1 (male), all suggesting separate phyletic origin.

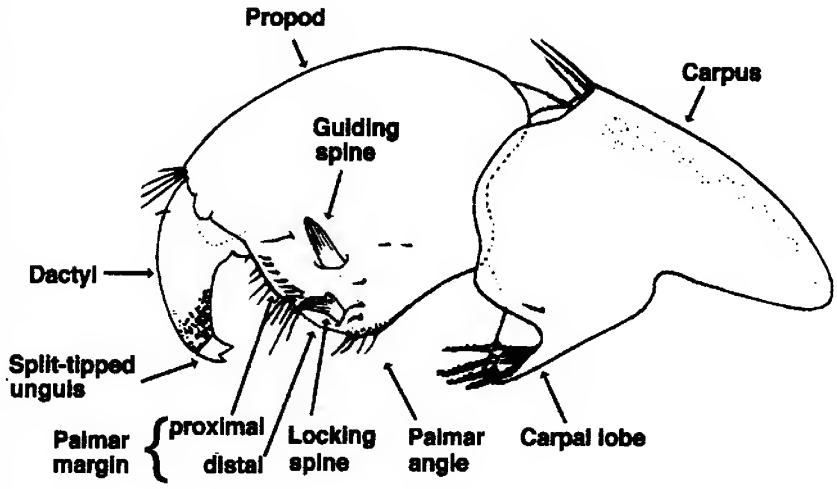
The Chiltoniinae continued to be recognized within family Ceinidae by Barnard & Barnard (1983) and Barnard & Karaman (1991). However, its principal subfamily character states, involving sexually dimorphic and other characters, do not conform with those of the type genus *Ceina.* Subfamily Chiltoniinae may therefore require separate family recognition within the Talitroidea, a proposal beyond the scope of the present study. Subfamily Hyalellinae is therefore here considered monotypic within family Hyalellidae.

Classificatory status of family Hyalellidae

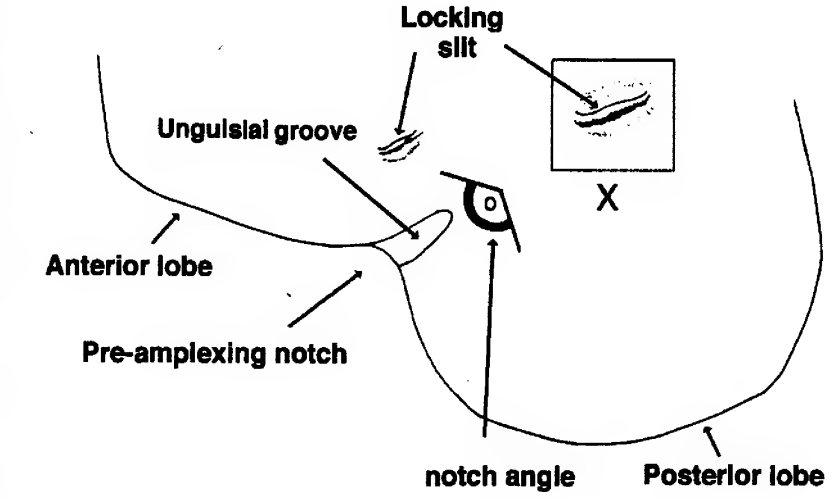
Barnard & Karaman (1991) have retained some

genera of family Hyalellidae within family Hyalidae (sens. lat.), apparently without formal numerical analysis. Laso-Wasem & Gable (2001) also include the genera *Parhyalella, Exhyalella,* and *Marinohyalella* within Hyalidae (sens. lat.). However, all genera of family Hyalellidae Bulycheva are reliably distinguished from all members of family Hyalidae (sens. str.) by the following character states: 1. Maxilla 1, palp vestigial or lacking (vs. distinct, 1-2 segmented); 2. Telson plate-like, apex entire or narrowly cleft (vs. fully bilobate, cleft to base).

Additionally within family Hyalellidae: coxae 1-4 are not posteriorly cuspate (vs. often distinctly cuspate); gnathopod 2 (male), carpal lobe is always present and distinct (vs. lacking or vestigial); peraeopods 3-7, distal segments are slender, weakly spinose (vs. stout, strongly spinose); peraeopods 5-7, bases lack posterior marginal "surge seta" and pit (vs. present); uropod 1, distomedial and distolateral peduncular spines ordinary (vs. often strongly developed); and uropod 3 uniramous, or ramus fused to the peduncle (vs. occ. unequally biramous, outer ramus not fused to peduncle). Sternal gills are present in one supergenus (*Hyalella*) (vs. lacking in all Hyalidae including freshwater members). Additionally, the preamplexing notch (female) is present in all genera and species of Hyalellidae and is highly variable in form (Figs. 1, 6). The preamplex-ing notch is yet known only within a few subgroups of Hyalidae and, when present, is relatively simple in form.



A. Gnathopod 1, inner face, male



B. Peraeon segment 2, left side, female

Fig. 1. Preamplexing morphology in mature males and females of *Allorchestes angusta* Dana.

Although accepted by Tzvetkova (1990), Barnard & Karaman (1991) did not recognize the new generic and species names proposed by Bousfield (1981) for North American Pacific species within families Hyalidae and Hyalellidae (e.g., within *Allorchestes).* Bousfield (2001) tentatively recognized them in a list of amphipod species of North America, but these names are herewith regarded as *nomena nuda* and suitably replaced in this study.

Characters and Character States.

In previous studies of hyalellid and hyalid amphipods, characters and states most frequently selected for species distinction have been those of the antennae, mouthparts, gnathopods, uropods, and telson (e.g., Barnard 1979; Ishimaru 1995). In this study of North Pacific hyalellids, those characters are also utilized, but the taxonomic significance of reproductive morphol-

KEY TO GENERA OF HYALELLIDAE

1. Gnathopods 1 - 2 (female) subsimilar in size and form; uropod 1, marginal spines of outer ramus few (1-2) or lacking; right and left mandibles, molar seta present; maxilla 1, palp 1-segmented . . 2.
   Gnathopods 1 - 2 (female) unlike in form and size; uropd 1, marginal spines of outer ramus well developed (3+); right and/or left mandible lacking molar seta; maxilla 1, palp essentially lacking . . . . . 4.

2. Telson lobes narrowly separated distally (telson cleft) . . . . . *Allorchestes* (p. 7)
   Telson lobes fused to apex (telson entire) . . . . . 3.

3. Sternal gills present; uropod 1, outer ramus with marginal spines, freshwater . . . . *Hyalella* (p. 26)
   Sternal gills lacking, uropod 1, outer ramus, marginal spines absent; marine . . . . . *Marinohyalella*

4. Antenna 2 (male), peduncle very stout, basal flagellar segments conjoint; maxilla 1, palp lacking; gnathopod 1 (male), unguis of dactyl often bidentate; one molar seta present . . *Parhyalella* (p. 28)
   Antenna 2 (male), peduncle normally thickened, basal flagellar segments distinct; maxilla 1, palp a single seta; gnathopod 1 (male), unguis of dactyl simple; both molar setae lacking; . . . . . *Exhyalella*

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ogy is emphasized. Thus, during preamplexus (precopulatory "carrying" of the female), the male grasps the female anteriorly, mainly utilizing gnathopod 1, but the "holding" action may be assisted by the stoutly enlarged antenna 2 (Lazo-Wasem & Gable 2001). Gnathopod 2 (male) may assist in positioning the female and in agonistically fending off other males (Borowsky 1984; Bousfield & Shih 1994). The dactyl of gnathopod 1 (male) apparently fits into a preamplexing "notch" located on the anteroventral margin of peraeon segment 2 of the female (Figs. 1, 6). The male dactyl and female "notch" are differently modified according to the species (Figs. 2, 6). The anterodistal palmar spines of the propod (male) may also be specialized as "guiding" and "locking" spines, presumably facilitating the grasping and holding action by the male (Fig. 1A). The form of the distal segments of gnathopods 1 & 2 of the male varies by species (Figs. 2,3). The corresponding portions of female gnathopods, used mainly in feeding and grooming, also vary according to the species (Figs. 4, 5).

Allorchestes Dana

Allorchestes Dana, 1849: 136. Dana 1853: 883. Stebbing 1906: 581. Bulycheva 1957: 111 (part). Barnard, 1974: 90. Bousfield, 1981: 81; 1996: 178. Bousfield 2001: 104.
non *Allorchestes* Chevreux & Fage (1925, part). Gurjanova (1951 part). Krapp-Schickel (1974, part).

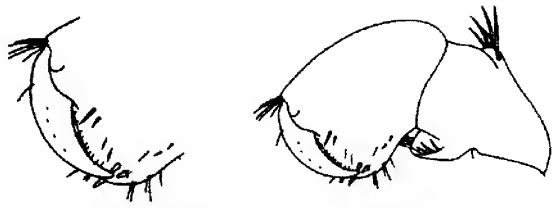
Type species: *Allorchestes compressa* Dana, 1853 (selected Chevreux & Fage 1925).

Species: Seven species occur in the North Pacific region, including 2 species new to science, and 1 resurrected (see Barnard & Karaman 1991: 367). *Allorchestes angusta* Dana, 1949 (= *A. oculatus* Stout, 1913?)(Alaska to California); *A. bellabella* Barnard,1974; Tzvetkova 1990 (Kamchatka, Aleutians to Oregon); *A. carinata* Iwasa, 1939 (Aleutians); *A. hirsuta* Ishimaru, 1995 (Sea of Japan); *A. malleola* Stebbing, 1899 (= *A. vladimiri* Derzhavin, 1937?)(Western Pacific shores, N. Japan and Sea of Okhotsk); ***A. priceae* n. sp.** (S.E. Alaska to southern British Columbia); and ***A. rickeri* n. sp.** (S.E. Alaska to Central California).
Incerta sedis: *Allorchestes japonica* Stimpson, 1855 (= *A. compressa* Dana fide Barnard & Karaman 1991, but listed separately by Ishimaru 1994.)
South Pacific: *Allorchestes compressa* Dana, 1853 (including *A. compressa* subsp. "W" Barnard 1974, and *A. compressa* subsp. "V" Barnard 1974); *A. novizealandiae* Dana, 1853 (see Hurley 1957).

Diagnosis: Body small to medium large, smooth or weakly carinate posterodorsally. Eyes medium, rounded. Antennae generally short, antenna 2 slightly the longer, peduncle (male) stouter than in female; gland cone small.

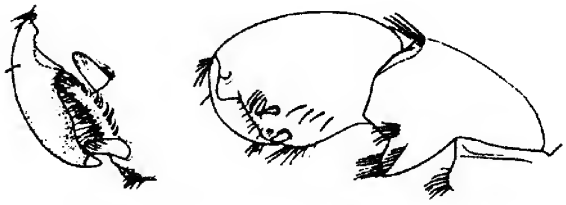
Mandible, left lacinia 5-6 dentate; both molar setae present. Maxilla 1, palp minute 1-segmented. Maxilliped palp, dactyl unguiform, without whip seta.

Coxae 1-4, posterior marginal cusp or process (acclivity of J. L. Barnard 1979) weak or lacking; coxa 4 large, broadly subquadrate. Gnathopods strongly sexually dimorphic. Gnathopod 1, carpus and propod usually hammer-shaped; dactyl often modified for

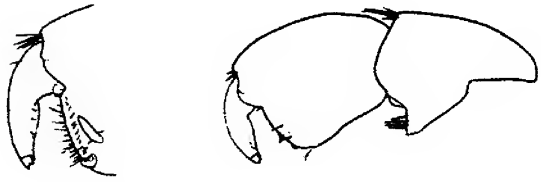


***A. compressa* subsp. V (per Barnard 1979)**

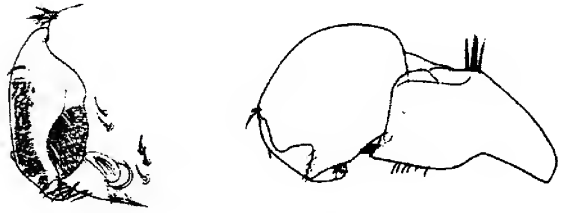
***A. novizealandiae* (Thomson, 1880) (per Hurley 1957)**



***A. carinata* Iwasa (per Barnard 1979)**



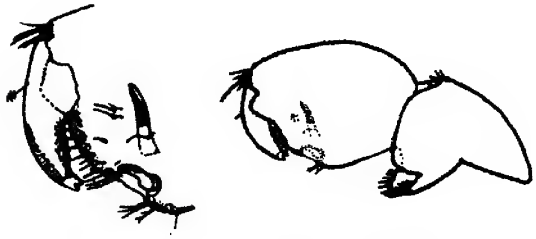
***A. hirsuta* Ishimaru, 1995**



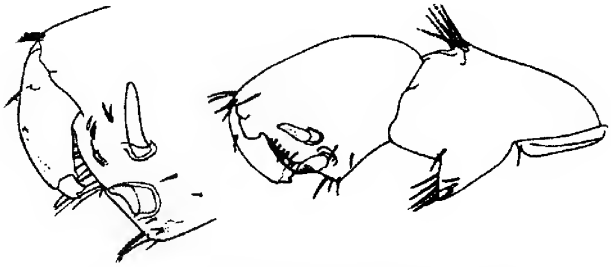
***A. bellabella* Barnard, 1974**

***A. priceae* n. sp.**

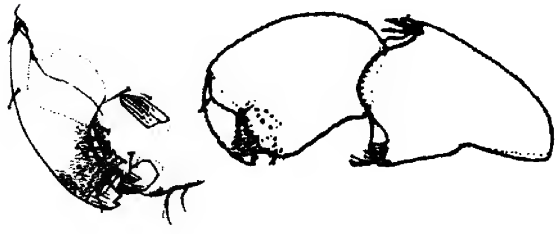
***A. angusta* Dana, 1856**



***A. malleola* Stebbing, 1899**

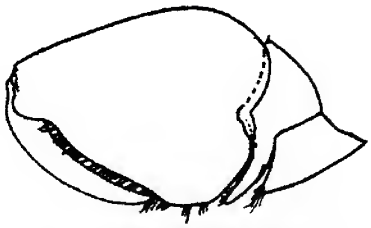


***A. angusta* Dana (per Barnard 1979)**

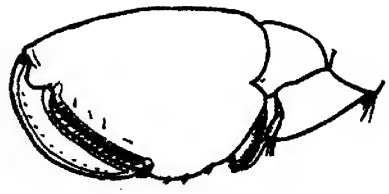


***A. rickeri* n. sp.**

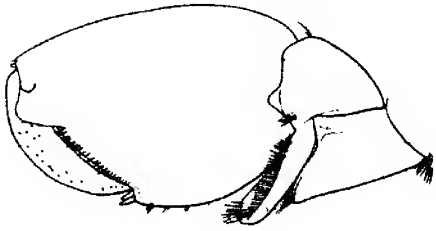
Fig. 2. *Allorchestes* spp. Male. Gnathopod 1. distal segments.



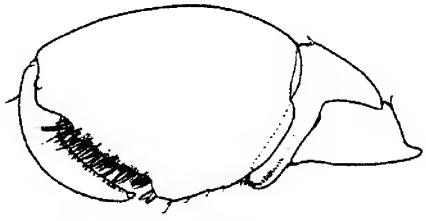
A. compressa subsp. V
(per Barnard 1979)



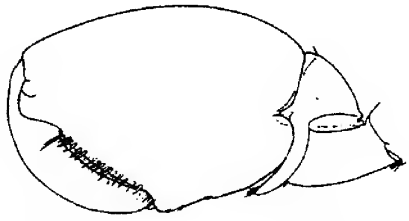
A. novizealandiae (Thomson, 1880)
(per Hurley 1957)



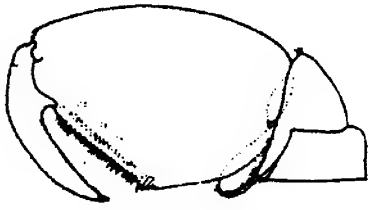
A. carinata Iwasa (per Barnard 1979)



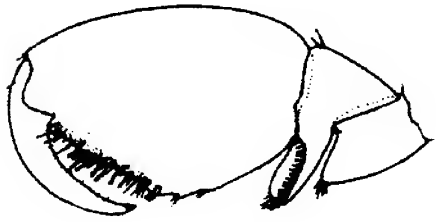
A. hirsuta Ishimaru, 1995



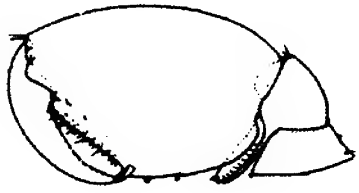
A. bellabella Barnard, 1974



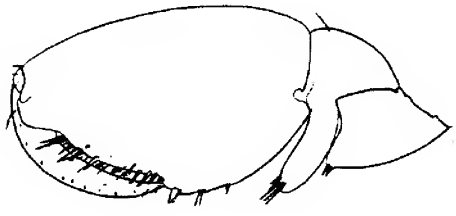
A. priceae n. sp.



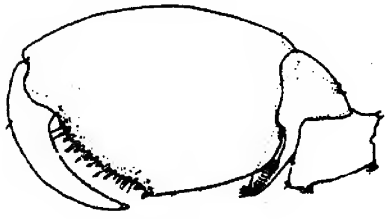
A. angusta Dana, 1856



A. malleola Stebbing, 1899



A. angusta Dana (per Barnard 1979)



A. rickeri n. sp.

Fig. 3. *Allorchestes* spp. Male. Gnathopod 2, distal segments.

KEY TO WORLD SPECIES OF *ALLORCHESTES*

(Character states of reproductive morphology illustrated in figures 1-6)

1. Gnathopod 1 (male), dactyl simple, unmodified; mostly South Pacific species ..... 2.
   Gnathopod 1 (male) dactyl modified, inflated or bifid, not simple; North Pacific only ..... 4.

2. Body dorsally smooth; P5-6 bases little broadened; South Pacific antiboreal only ..... 3.
   Pleon mid-dorsally carinated; P5-6, bases broadened, rounded behind; North Pacific only. . .
   ..... *A. carinata* Iwasa (p. 13)

3. Gnathopod 1 (male), dactyl exceeding toothed palm ..... *A. novizelandiae* group
   Gnathopod 1 (male), dactyl normal, not exceeding regular palm ..... *A. compressa* group

4. Gnathopod 1 (male); dactyl inflated, as long as palm, unguis simple; propod palm processiferous; peraeopods segments, corners with multiple blunt striated spines..... .5.
   Gnathopod 1 (male); dactyl not inflated, shorter than palm; unguis bifid; palm smoothly convex; peraeopods 5-7, hind corners of segments 4 & 5 with few simple spines only ..... 6.

5. Gnathopod 1 (male) dactyl very inflated, little longer than wide; propod palmar process subacute; coxa 4 squarish; urosome 1 not (or weakly) carinated; maxilliped palp dactyl short, nail long . .
   ..... *A. bellabella* Barnard (p. 14)
   Gnathopod 1 (male) dactyl slightly inflated, distinctly longer than wide; propod palmar process bluntly rounded; coxa 4 broadly rounded below; urosome 1 distinctly carinated; maxilliped palp, dactyl slender, longer than segment ..... ***A. priceae* n. sp.** (p. 16)

6. Uropod 1, outer ramus with marginal spines; antennae elongate; gnathopod 2 (male) palm submarginally lined with long setose; telson squarish, deeply cleft ..... *A. hirsuta* Ishimaru (p. 18)
   Character states not so ..... 7.

7. Uropod 3, ramus blunt, short (~1/2 length of peduncle); gnathopod 2 (male), propodal palm submarginally with slender spines; western Pacific ..... *A. malleola* (p. 20)
   Uropod 3, ramus tapering, subacute, length about equal to peduncle; gnathopod 2 (male), palmar margin lined with short spines; eastern Pacific ..... 8.

8. Peraeopod 5, segment 4 normal, length longer than width; angle of preamplexing notch broadly obtuse..... *A. angusta* (p. 24)
   Peraeopod 5, segment 4 broadened, width = length; angle of preamplexing notch (female) nearly right-angled ..... ***A. rickeri* n. sp.** (p. 25)

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preamplexus with female. Gnathopod 2 (male) large, carpal lobe large, inner margin with comb setae.

Peraeopods 3-7 regular, slender, weakly spinose; posterior margin of basis lacking "surge seta" and pit; marginal spines simple or striate, locking spines absent; dactyls short, unarmed.

Epimeral plate 2 deepest; pleopods with 2-3 peduncular retinacula. Uropod 1, peduncle often lacking distal outer marginal spines; outer ramus usually lacking marginal spines. Uropod 2, outer ramus the shorter. Uropod 3 uniramous, ramus short, apex with setae and spine(s).

Telson plate-like, apically notched, lobes separated distally but not diverging.

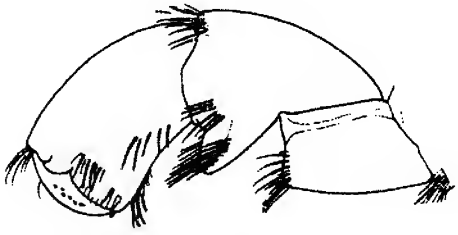
Coxal gills sac-like, subequal. Sternal gills lacking.

Female: Precopulatory notch of peraeon segment 2 large, variable, often complex; locking slit also present in more advanced species. Brood plates narrowly spade-shaped to subrectangular, marginal setae short.

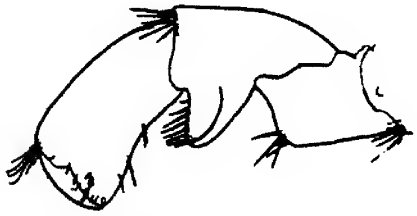
Distributional Ecology: Species of *Allorchestes* Dana are restricted almost exclusively to the Pacific Ocean. The animals occur mainly in mats of algae and sea grasses along the open coast or in semi-protected

***A. compressa* subsp. V**
(per Barnard 1979)

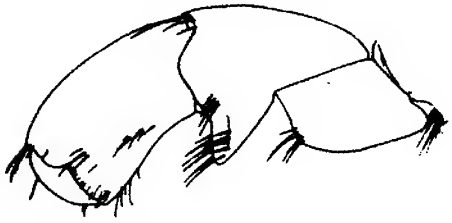
***A. novizealandiae* (Thomson, 1880)**
(per Hurley 1957)



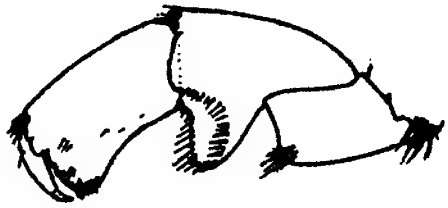
***A. carinata* Iwasa (per Barnard 1979)**



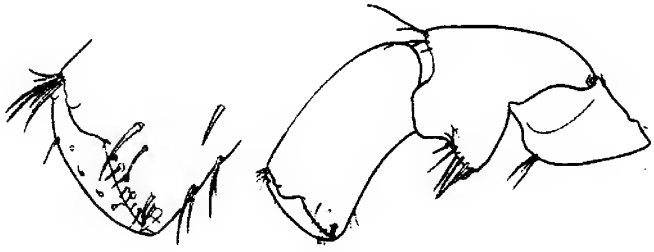
***A. hirsuta* Ishimaru, 1995**



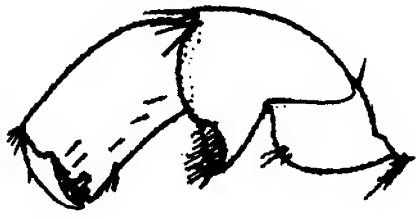
***A. bellabella* Barnard, 1974**



***A. priceae* n. sp.**



***A. angusta* Dana (per Barnard 1979)**

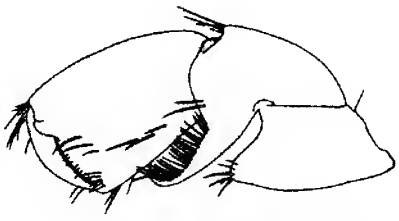


***A. malleola* Stebbing, 1899**

***Hyalella azteca* (Saussure, 1858)**

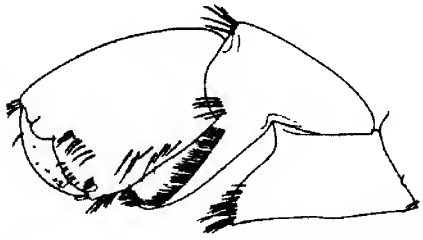
***A. rickeri* n. sp.**

Fig. 4. *Allorchestes* and *Hyalella* species. Gnathopod 1(female) , distal segments.

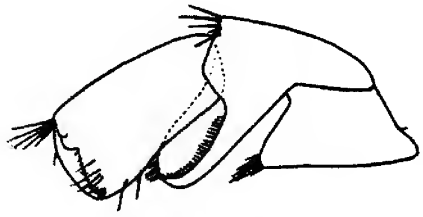


A. compressa subsp. V
(per Barnard 1979)

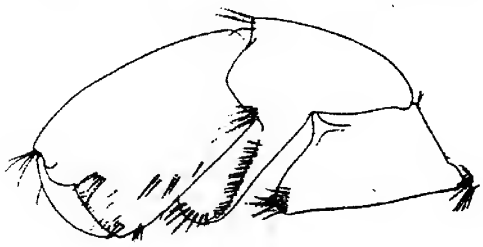
A. novizealandiae (Thomson, 1880)
(per Hurley 1957)



A. carinata Iwasa (per Barnard 1979)

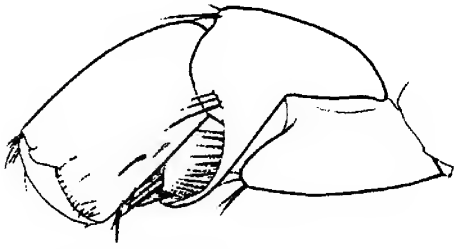


A. hirsuta Ishimaru, 1995

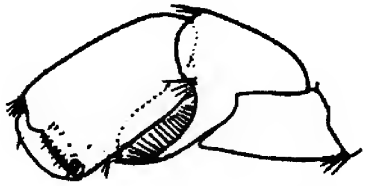


A. bellabella Barnard, 1974

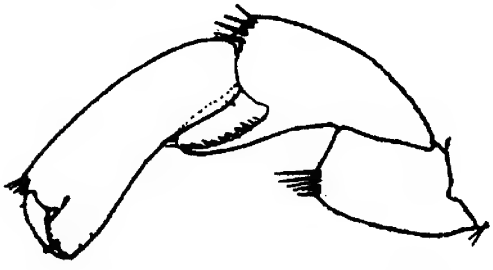
A. priceae n. sp.



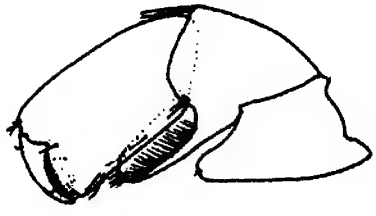
A. angusta Dana (per Barnard 1979)



A. malleola Stebbing, 1899



Hyalella azteca (Saussure, 1858)



A. rickeri n. sp.

Fig. 5. *Allorchestes* and *Hyalella* species. Gnathopod 2 (female) , distal segments.

shallows, from the lower intertidal zone to a depth of about 30 metres.

According to Barnard (1979:90), known species are endemic to cooler waters of north and south Pacific regions and the genus, as presently constituted, therefore exhibits bipolar discontiguity. Subsequent description of other new species, and current studies on this genus and on diverse generic groupings within the Hyalidae tend to confirm this conclusion (Hendrycks & Bousfield, in prep.).

However, no species of *Allorchestes* sens. str. occur in both the north and south Pacific regions or elsewhere. Thus, all previous species allocations in the North Atlantic region (e.g., in Chevreux & Fage 1925) have subsequently been transferred to generic subgroupings within Hyalidae (see also Barnard 1974; Krapp-Schickel 1974; 1993; Bousfield 1981; Lazo-Wasem & Gable 2001).

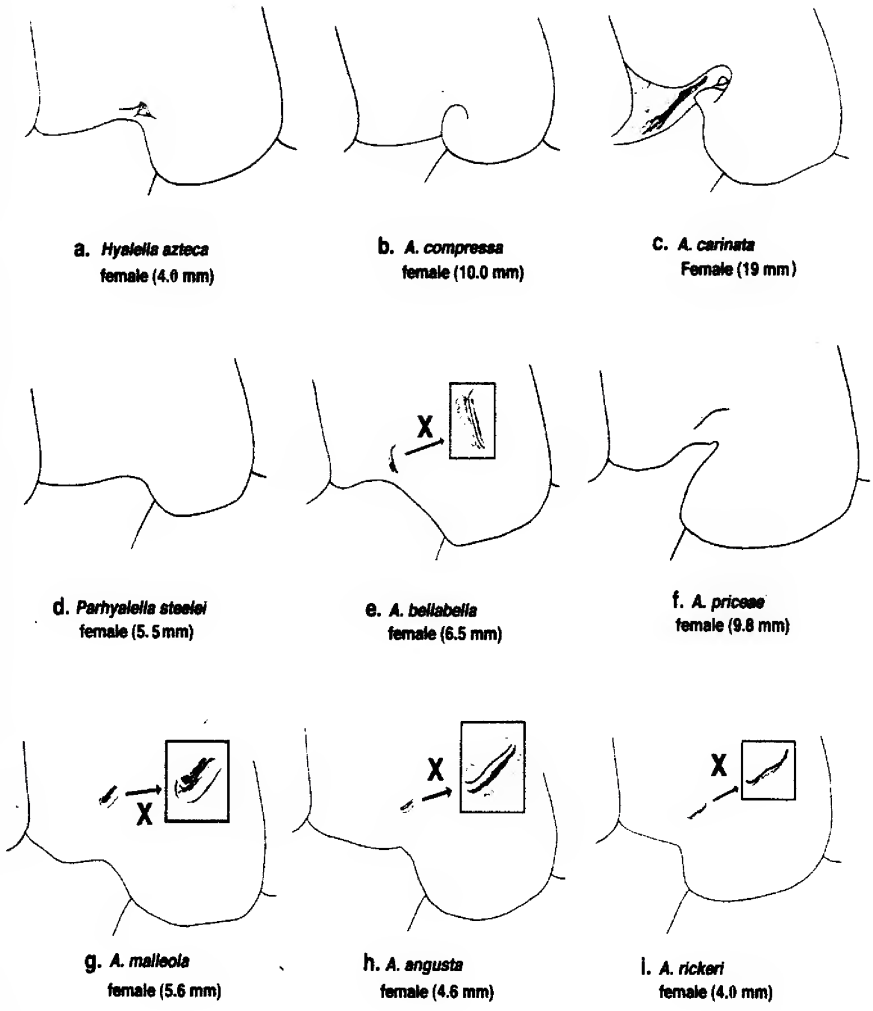


Fig. 6. Preamplexing notch of peraeon segment 2 of mature females of *Allorchestes* and other genera of family Hyalellidae.

Remarks: Several species of the Australian-New Zealand region have been synonymized with *Allorchestes compressa* Dana (an unclarified species, fide Barnard, 1974), but such action may have doubtful validity. CMN material collected by ELB and attributed to *A. compressa,* is relatively large, smooth-bodied, and unlike species of the North Pacific complex. *Allorchestes novizealandiae* (Thomson) also has several synonyms (Barnard & Karaman 1991: 381). In both southern species complexes, preamplexing morphological modification of the male gnathopods are unlike those for North Pacific counterparts, and in some populations, the degree of distal fusion of the telson lobes appears variable within males and females of the same species (authors' unpublished data).

Except for its completely fused telson lobes, the genus *Marinohyalella,* embracing the single species *M. richardi* from the Mediterranean region, appears virtually identical with genus *Allorchestes.*

Allorchestes carinata Iwasa
(Figs. 2, 3, 4, 5, 6c, 7)

Allorchestes malleolus carinatus Iwasa, 1939: 288-289, figs. 23, 24, pl. 21. Bulycheva 1857: 118-120, fig. 44. *Allorchestes carinata* Barnard, 1979: 96-98, fig. 54. Bousfield 1981: 81, figs. 12, 13. Tzvetkova, 1990: 45-47, figs. 5-6. Barnard & Karaman 1991: 387.

Material Examined: Bering Sea & Aleutians, Alaska: Stn. TSC-1, Square Bay, Cyril Cove, Amchitka, Aleutian Islands, K. Chew coll., 1968 - 5 ♂♂ (1 slide mount?); 6 ♀♀ ov, NMNS Acc. 1976-30; Ibid., coll. J. Pahnisona, 1971 - 1 ♀ (slide mount) CMN ??; Dock at Constantine Harbor, Amchitka I., C. E. O'Clair coll., 1968 - 1 ♂ (damaged (slide

mount) - MNNS Acc. No. 1976-30; Ibid., - 1 ♂ (23 mm) (slide mount)(fig'd. specimen), 1 ♀ ov (22 mm) (slide mount)(partly fig'd) + 3 ♂♂. CMN Acc. 1976-30; Transect Plot #4, Mt. 4, St. Makarios Bay, Amchitka I., G. J. Tutmark, C. E. O'Clair coll., 1969 - 1 ♂, 1 ♀ ov. CMN Acc. No. 1976-30; Ibid., 1 ♀, CMN Acc. No. 1976-301.

Diagnosis: Male (23.0 mm). Body large, conspicuously carinate mid-dorsally on posterior peraeon, pleon and urosome 1. Head regular. Eyes medium, subreniform, black. Antennae medium long. Antenna 1, flagellum 16-20 segmented. Antenna 2, flagellum 13-16-segmented, distal segments slender.

Mandible: left lacinia 5-dentate; spine rows with 3 blades. Maxilla 1, palp medium. Maxilla 2, inner plate regular, marginal plumose seta strong. Maxilliped, inner plate with oblique apex; outer plate medium; palp segments 2 & 3 broad, massive; dactyl short, stout.

Coxal plates 1-3 broadly rectangular, coxa 3 with slight posterior marginal cusp. Coxa 4 as broad as deep, lower margin slightly convex. Coxa 5 shallow, aequilobate. Coxal gills relatively large, sac-like, smallest on gnathopod 2.

Gnathopod 1, carpal lobe medium-deep, distal margin with ~30 long comb setae; propod medium deep, broadening distally, palm smooth, nearly transverse; guiding spine short, inset at an angle to palm; dactyl stout, moderately thickened proximally, unguis relatively large, simple, closing on locking spine at posterodistal angle. Gnathopod 2, carpal lobe large, lined distally with ~40 medium comb-spines; propod, palm short, straight, lined with double row of short spines.

Peraeopods 3 & 4, segment 6 lined with 3-5 singly inserted spines. Peraeopods 5-7, bases wider than deep, rounded behind; segments 4-5 slightly broadened, postero-distal apices with clusters of short blunt striated peg-spines; segment 6 lined anteriorly with 4-5 pairs of short spines; dactyls stout.

Epimeral plates 2 deepest; plates 2 & 3, hind corners squarish, not produced. Pleopods large, peduncles with 2 retinacula. Marginal spines of peduncle of uropod 1 lacking distally, of uropod 2 regularly spaced; rami sublanceolate, with stout terminal spine; outer ramus lacking marginal spines. Uropod 3, peduncle stout, with 3 stout distal spines; ramus short, thick, apex subtruncate, bearing single spine and several short finely pectinate setae.

Telson squarish, lobes narrowly cleft 1/3 to base.

Female ov (19.3 mm): Peraeon segment 2 (Fig. 6) with large squarish preamplexing notch; unguisial groove relatively broad,deep; locking slit lacking; postero-distal lobe large, deep. Gnathopod 1, carpal lobe medium, distally with ~20 longish comb-spines; pro-pod medium deep, length subequal to carpus, palm gently convex, nearly vertical. Gnathopod 2, carpal lobe large, deep, with numerous (~50) medium comb-spines; propod medium deep, palm slightly oblique.

Brood plates on gnathopod 2 large, broad, margins with numerous short fine hooked setae.

Distributional Ecology; Subarctic and boreal pan-Pacific, from the northern Sea of Japan, Okhotsk Sea,and Kamchatka peninsula through Bering Sea and the Aleutian island chain to SE Alaska and northern B. C. Inhabits predominantly littoral and uppermost sublittoral zones (Barnard 1974). Specimens from the shores of Olga Bay, eastern Kamchatka, occurred on sandy, stony and rocky sediments, at depths of 0.5 - 4 m. (Tzvetkova 1990).

Remarks: *Allorchestes carinata* is a morphologically primitive species, superficially distinguished by its large size, mid-dorsal low posterior carinations, and stout clavate spines on the peraeopods. In most character states this large species appears intermediate between members of the North and South Pacific generic subgroupings (Fig. 17).

Allorchestes bellabella Barnard
(Figs. 2, 3, 4, 5, 6e, 8)

Allorchestes bellabella Barnard, 1974: 43. Barnard 1979: 94, figs. 52(part), 53. Bousfield 1991: 81, figs. 12, 13. Austin 1985: 594. Tzvetkova 1990: 40-45, figs. 3-4. Barnard & Karaman 1991: 367.
Allorchestes subcarinata Bousfield, 1981: 81, figs. 12, 13. Bousfield 2001: 104.
non *A. angusta* Barnard 1954: 21-23.

Material Examined: 41 males, 61 females, in 19 lots, from Aleutians and SE ALASKA to Southern B.C. (see map, fig.18).
Alaska: Plot 1A2, #19, Amchitka I., Aleutians, C. E. O' Clair, coll., 1971 - 1 ♀?
SE Alaska, ELB Stns., June-July, 1961: A16, South side Port McArthur Bay, Kuiu I - 18 ♂♂, 23 ♀♀ (mostly ov.); A32, Wood Spit, Holkam Bay - 3♂♂ (1 slide mount) (fig'd. specimen); 2 ♀♀, NMNS 61-123; A71, Ankau Creek mouth - 1 ♂, 3 ♀♀ ov; A75, Kayak I., Wingham I, 1 ♀ ov (slide mount); A 80, Nuchek Beach, Hinchenbrook I., 2 ♂♂ (1 slide mount), 1 ♀ (slide mount); A136, Head of Thumb Bay, Resurrection Bay - 1 ♂, 1 ♀; A171, Puffin Bay, Baranof I. (2 lots) - 1 ♂, 4 ♀♀.

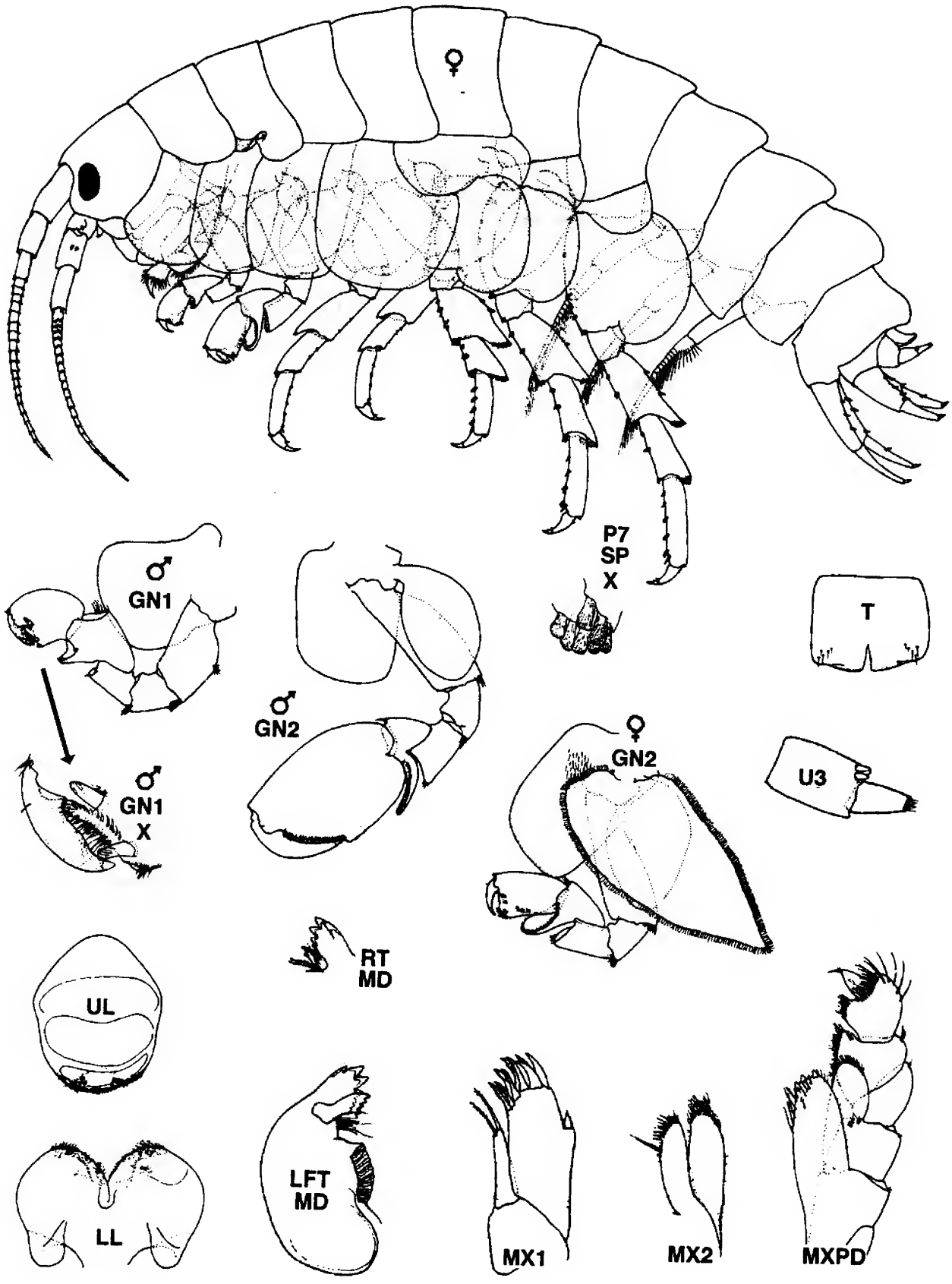


Fig. 7. *Allorchestes carinata* Iwasa, 1939. Male (23.0 mm); female 19.3 mm). Low Intertidal, Amchitka, Alaska.

British Columbia
Queen Charlotte Islands, ELB Stns., July, 1957.
H2, Kiusta Village, Parry Passage - 1 ♂, 14 ♀♀.
North Central Coast, ELB Stns, July, 1964:
H4, Baker Pt., Aristazabel I., - 1 ♂; H23 Deadman's Cove, (2 lots) - 4 ♂♂, 2 ♀♀.
Southern Vancouver I. , ELB Stns, July, 1977.
B5a, Witty's Lagoon - 2 ♂♂ (slide mount, fig'd specimen), 5 ♀♀ (1 slide mount, partly fig'd); NMCC 1883-1520.

Diagnosis: Male (6.0 -10 mm). Body medium large, very slightly carinate mid-dorsally on pleon segments 1-3. Head regular. Eye broadly subreniform, black. Antennae medium long. Antenna 1, flagellum 9-14 segmented. Antenna 2, flagellum 11-15 segmented, distal segments slender.

Mandible: left lacinia 5 1/2-dentate; left spine row with 3 blades, right with 2 blades. Maxilla 1, palp medium, distinct. Maxilla 2, inner plate regular, marginal plumose seta strong. Maxilliped, inner plate with oblique apex; outer plate medium; palp segments 2 & 3 not enlarged; dactyl short.

Coxal plates 1-3 each with slight posterior marginal cusp, coxae 2-3 deeply subquadrate, lower margins gently rounded. Coxa 4 as broad as deep, lower margin convex. Coxa 5 shallow, aequilobate. Coxal gills medium, sac-like, subequal, slightly smallest on gnathopod 2.

Gnathopod 1, carpus shallow, posterior lobe lined distally with ~15 short comb-setae; propod medium deep, narrowing slightly distally to a transverse palm that is produced sharply forward at the posterodistal angle; propodal guiding spine short, set nearly horizontally above the posterior margin; propodal locking spine short, set horizontally at base of palmar process; dactyl strongly inflated, unguis small, simple, closing below locking spine. Gnathopod 2, carpal lobe large, with ~30 medium long marginal comb-setae; propod, posterior margin relatively short, distally straight; palm straight, submarginally lined with double row of medium spines; dactyl lined posteriorly with ~20 spinules.

Peraeopods 3 & 4, posterior margin of segment 6 with 3-4 singly inserted complex spines. Peraeopods 5-6, bases not wider than deep, rounded behind; segments 4-5 broadened distally, posterodistal apices with cluster of striated peg-spines; dactyls stout. Peraeopod 7, basis broadening posterodistally; posterodistal lobe truncated; segment 6, anterior margin lined with 4-5 pairs of spines.

Epimeral plate 3, hind corner slightly acuminate. Pleopod peduncles with 2 retinacula. Uropods1 & 2, outer marginal spines of peduncle regularly spaced; rami slightly tapering, outer ramus lacking marginal spines. Uropod 3, peduncle medium stout, with 2 distally striated spines; ramus medium short, thick, tapering to blunt apex bearing 1 small spine and 8-10 short setae.

Telson squarish, lobes narrowly cleft 1/4 to base.

Female (5.0 mm): Peraeon segment 2 (Fig. 6) with large regularly concave preamplexing notch; unguisial groove lacking; locking slit short, vertical, dorsad of mid-point of notch; postero-distal lobe large, deep. Gnathopod 1, carpal lobe medium, distally with ~20 longish comb spines; propod medium deep, length subequal to carpus, palm very slightly parachelate. Gnathopod 2, carpal lobe large, deep, lined marginally with ~40+ medium comb-spines; propod medium deep, palm slightly convex.

Brood plates medium large, margins with numerous short fine hooked setae.

Distributional Ecology: Tzvetkova (1990) encountered live material on rocky and sandy sediments in Olga Bay, Kamchatka, at depths from 1.2 - 12 m. Females (7-10 mm) with eggs in the marsupium were noted on 16 Aug., 1975 (Tzvetkova 1990). Known from islands of Beringia, Aleutian Islands, S. E. Alaska and B. C. south to Oregon, sometimes encountered in the littoral plankton (Barnard 1979).

Remarks: The propod of gnathod 1 (male), with strong posterio-distal tooth, inflated dactyl, and simple unguis is distinctive of the species. It appears most closely related to *A. priceae* (Figs. 9, 17).

Allorchestes priceae n. sp.
(Figs. 2,3,4,5,6f, **9**)

Allorchestes urocarinata Bousfield, 1981: 81, figs. 12, 13. (nomen nudum).—Bousfield 2001: 104.

Material Examined: SE Alaska, ELB Stns., 1961:
A171, Puffin Bay, Baranof I., July, 1980 - **Holotype** ♂, (slide mount), CMNC 2001-0025; **Allotype** ♀ (slide mount) CMNC 2001-0026, 1 ♂, 1 ♀ **Paratypes**, CMNC 2001-0027.
Ibid. - ~120 juvenile and immature specimens, Topotypes.
British Columbia:
Queen Charlotte Islands ELB Stns., 1957:
Stn. H2, Langara I., Queen Charlotte Islands - several immature specimens (possibly misidentified as *A. bellabella*?)
Southern Vancouver I., ELB Stns., 1970:
Botanical Beach, Cape San Juan, low intertidal sand and algae, July - 1 ♂, 1 ♀.

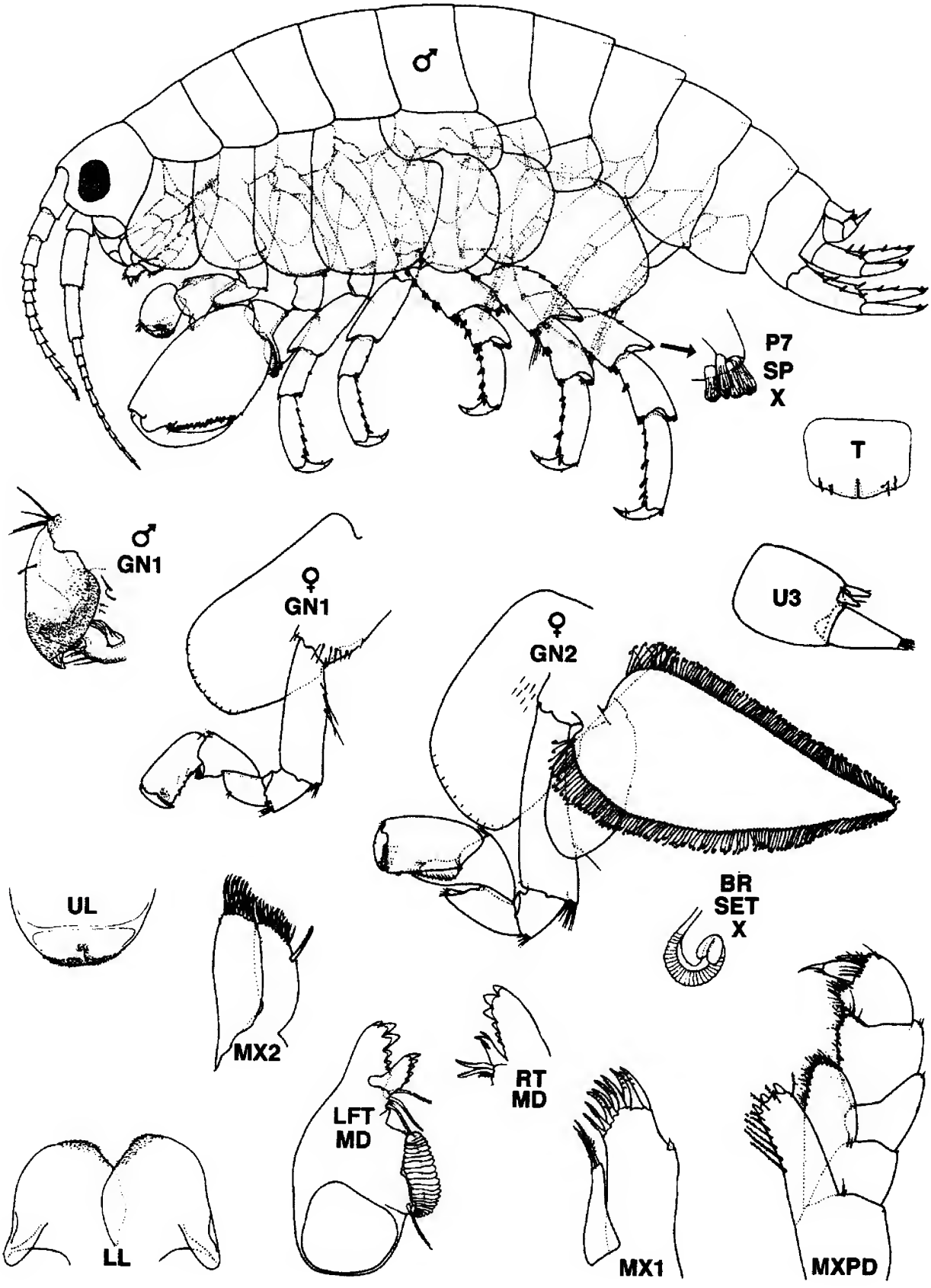


Fig. 8. *Allorchestes bellabella* Barnard, 1974. Male (6.0 mm); female (5.0 mm). Witty's lagoon, Vancouver I., B. C.

Diagnosis: Male (13.0 mm). Body medium large, conspicuously carinate mid-dorsally on urosome segment 1. Head regular. Eye medium large, broadly subreniform, black. Antennae medium long. Antenna 1, flagellum 16-17 segmented. Antenna 2, flagellum 13-segmented, distal segments slender.

Mandible: left lacinia 5 dentate; right spine row with 3 blades. Maxilla 1, palp medium. Maxilla 2, inner plate regular, marginal plumose seta strong. Maxilliped, inner plate with oblique apex; outer plate medium; palp segments 2 & 3 broad, massive, dactyl slender.

Coxal plates 1-3 each with slight posterior marginal cusp, lower margins gently rounded. Coxa 4 as broad as deep, lower margin strongly convex. Coxa 5 shallow, aequilobate.

Gnathopod 1, carpus deep; propod medium deep, broadening distally to transverse palm having rounded tumescent posterodistal process; median amplexing tooth striated, set at angle to palm; dactyl moderately thickened medially, unguis small, simple. Gnathopod 2, carpal lobe large, with short marginal comb-setae; propod, posterior margin relatively short, distally straight; palm straight, lined with short spines.

Peraeopods 3 & 4, posterior margin of segment 6 with 3-4 groups of small complex spines. Peraeopods 5-7, segments 4-6 little broadened, margin and apices with cluster of short blunt peg-spines.

Epimeral plates 2 & 3, hind corners slightly acuminate. Uropods 1 & 2, outer marginal spines of peduncle regularly spaced; outer ramus lacking marginal spines. Uropod 3, ramus medium short, thick, apex blunt, with short setae.

Telson squarish, lobes narrowly cleft 1/3.

Female ov (9.8 mm): Peraeon segment 2 (Fig. 6) with medium large sharply concave preamplexing notch; unguisial groove large, broad, deep, narrowing sharply; locking slit medium long, oblique, set dorsad of unguisial groove; posterodistal lobe large, deep, strongly convex anteriorly.

Gnathopod 1, carpal lobe medium, distally with long comb-spines; propod medium deep, length subequal to carpus, palm gently convex, transverse. Gnathopod 2, carpal lobe large, deep, with numerous medium comb-spines; propod medium deep, palm slightly oblique.

Brood plates medium large, margins with numerous short fine hooked setae.

Etymology: The species is named in honour of Judith C. Price, CMN assistant collections manager of crustaceans, whose ready help in recording, retrieving, and cataloguing has greatly expedited the description of many new taxa in the museum collections of Pacific coastal marine amphipods.

Distributional Ecology: Recorded at outer coastal stations from SE Alaska, the Queen Charlotte Islands, and southern Vancouver I., in coarse sands of the lower intertidal and inshore shallows. The distribution is limited narrowly within SE Alaska to southern B. C., but might also be expected in suitable coastal habitats of the northwestern United States.

Remarks: This medium-sized species is distinctive in its relatively long, slender antennae, mid-dorsally carinated urosome segment 1, and partly swollen simple-tipped unguis of gnathopod 1 (male). In balance of character states it appears most closely allied with *A. bellabella* Barnard (see also Fig. 17).

Allorchestes hirsuta Ishimaru
(Figs. 2, 3, 4, 5, **10**)

Allorchestes hirsuta Ishimaru, 1995: 46, figs.1-4.

Material Examined: None.

Diagnosis: Male (10.3 mm). Female ov (10.0 mm). Ishimaru (1995) has provided full description and figures of both sexes of this medium sized species from the southern Sea of Japan. His figures, some of which are reproduced here, also illustrate character states of pleopods, brood plates, and other appendages that are of generic as well as species diagnostic signficance, and seldom figured and/or descibed by other authors.

Dr. Ishimaru did not illustrate the preamplexing notch of the female of *A. hirsuta.* However, he did examine this taxonomic feature and believed "the notch of *A. hirsuta* (to be) relatively similar to that of *A. rickeri,* (but) is subacute and smaller" (pers. com.).

Distributional Ecology: On floating *Sargassum* north of Oki Island, southern Japan Sea. Not yet known from the North American Pacific coast.

Remarks: The species belongs to the North Pacific cluster of relatively small advanced species having hammer- shaped male gnathopod 1 with split-tipped unguis. It differs from *A. angusta* Dana in the elongate antennae, strongly setose palmar margin of gnathopod 2 (male), carinate urosome, and marginally spinose outer ramus of uropods 1 & 2, among other character states.

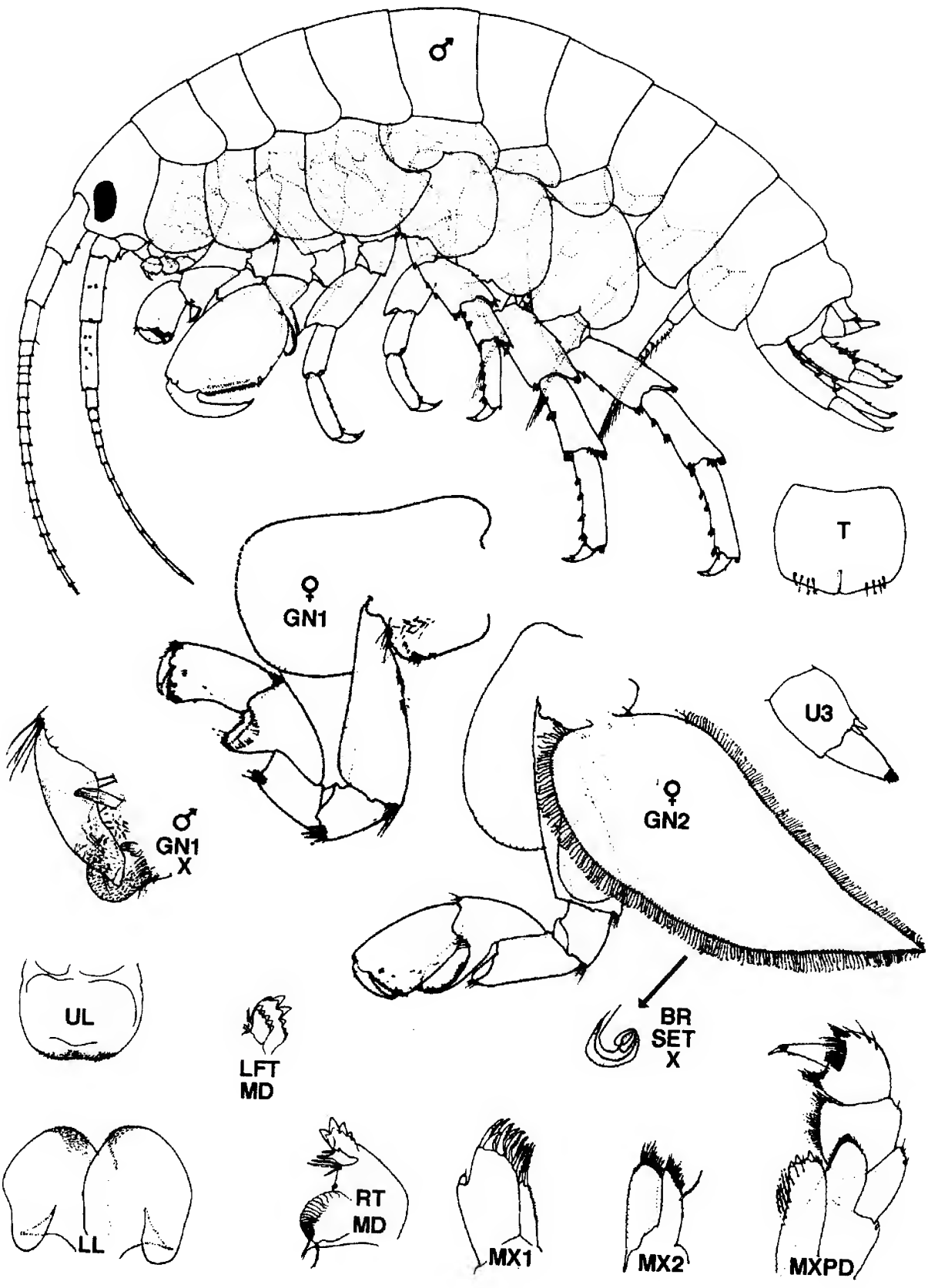


Fig. 9. ***Allorchestes priceae* n. sp.** Male (13.0 mm); female ov (12.0 mm). Stn A170, Puffin Bay, Baranof I., SE Alaska.

Allorchestes malleola Stebbing
(Figs. 2, 3, 4, 5, 6g, 11)

Allorchestes malleolus Stebbing, 1899: 409, pl. 33A. Iwasa 1939: 285, figs. 20-22. Tzvetkova 1967: 183. Bousfield 1981: 81, figs 12, 13. Ishimaru 1994: 67.
Allorchestes vladimiri Derzhavin, 1937: 95-95, pl. 5 fig. 2. Gurjanova 1951: 822, fig. 575. Bulycheva 1957: 115, fig. 43.

Material examined: USSR: Stn. 1, Anama Bay, Shikotan, S. Kurile I., O. G. Kussakin coll., July 5, 1955 - 2♂♂ (1 slide mount), (fig'd specimen); 3 ♀♀ (1 slide mount), NMCC, ACC 1979-267.
Japan: Usuziri, Hokkaido, A. Hirayama coll., June 26/78 - ♂ (9.0 mm) (slide mount), ♀ ov (8.0 mm (slide mount), CMN collns.

Diagnosis: Male (5-9 mm). Body medium, middorsally smooth. Head regular. Eye medium large, broadly subreniform, black. Antennae short to medium. Antenna 1, flagellum 9-12 -segmented. Antenna 2, flagellum 9-10-segmented.

Mandible: left lacinia 5 1/2 dentate; spine rows with 2-3 blades. Maxilla 1, palp medium. Maxilla 2, inner plate regular, marginal plumose seta strong. Maxilliped, inner plate with oblique apex; outer plate medium broad; palp segments 2 & 3 broad, massive, dactyl slender.

Coxal plates 2-3 subrectangular, each with slight posterior marginal cusp. Coxa 4 squarish, not wider than deep Coxa 5 shallow, aequilobate. Coxal gills medium large, subequal, sac-like, slightly smallest on gnathopod 2

Gnathopod 1, carpal lobe medium, lower margin lined with ~12+ medium-long split-tipped, finely pectinate comb setae; propod medium deep, broadening distally to nearly vertical palm that is proximo-medially convex; guiding tooth striated, elongate, set vertically (parallel to, or at a slightly reverse oblique angle) to palm, locking spine shorter, slightly sinuous, tip reaching lower palmar margin; dactyl short, moderately thickened proximally, unguis small, tip unequally bifid, closing above the locking spine. Gnathopod 2, carpal lobe large, with ~20 short marginal comb-setae; propod, posterior margin relatively short, distally straight; palm straight, submarginally lined with double row of short spines; dactyl, inner margin lined with fine spinules.

Peraeopods 3 & 4, posterior margin of segment 6 with 3-4 small spines. Peraeopods 5-7, bases broad, (broader than deep in peraeopod 7), hind margin weakly scalloped; segments 4-5 slightly broaded distally, posterodistally produced, apices with clusters of distally striated spines; segment 6, anterior margin with 3-4 pairs of spines; dactyls medium short.

Epimeral plates 2 & 3, hind corners sligthly acuminate, not produced. Pleopod peduncles with 3 retinacula. Uropods1 & 2, rami tapering, apex with 1 stout striated spine and several small accessory spines; outer ramus lacking marginal spines; peduncle of uropod 1 lacking marginal spines in distal half. Uropod 3, peduncle short, deep, with 2-3 stout, striated, apicodistal spines; ramus medium short, thick, apex blunt, armed with 1 spine and 6 finely pectinate short setae.

Telson squarish, lobes narrowly separated, cleft 1/3-1/2 to base.

Female ov (4.5-8 mm): Peraeon 2, pre-amplexing notch shallow, angle very obtuse (140°+); ratio of anterior:posterior lobes about 45:55); locking slit directly dorsad. Coxal plates large, deep; coxa 4 deeper than broad.

Gnathopod 1, carpal lobe medium, distally with ~14 longish finely split-tipped comb spines; propod medium deep, length about twice depth and slightly longer than carpus, palm very slightly parachelate. Gnathopod 2, carpal lobe large, deep, distally line with ~24 medium comb-spines; propod slightly deeper than in gnathopod 1, palm transverse.

Brood plate on peraeopod 2 large, distally sharply acute; margins with numerous medium length setae.

Distributional Ecology: Northern Sea of Japan, Okhotsk Sea, to Kamchatka (Tzvetkova) low intertidal to depth of 3-4 m (Derzhavin). Aleutian islands to SE Alaska?

Remarks: This species has been synonymized with *A. angusta* Dana, 1856, which it most closely resembles. However, it is reliably distinguished by morphogical characters of the key (p. 10), and by its non-overlapping distribution in the central North Pacific region.

Bulycheva's (1957) figures of the body, uropod 3 and telson identified by her as *A malleolus* Stebbing, 1899, are apparently adapted directly from Derzhavin's figures of the 6-7 mm holotype male and 7-8 mm allotype female of *A. vladimiri*. However, her individual (enlarged) figures of the antennae, gnathopods, peraeopods, and mouthparts may have been taken from another specimen and possibly another species, since significant differences may be discerned between her figures and the corresponding individual figures of Derzhavin (1937). Since this material has not been re-

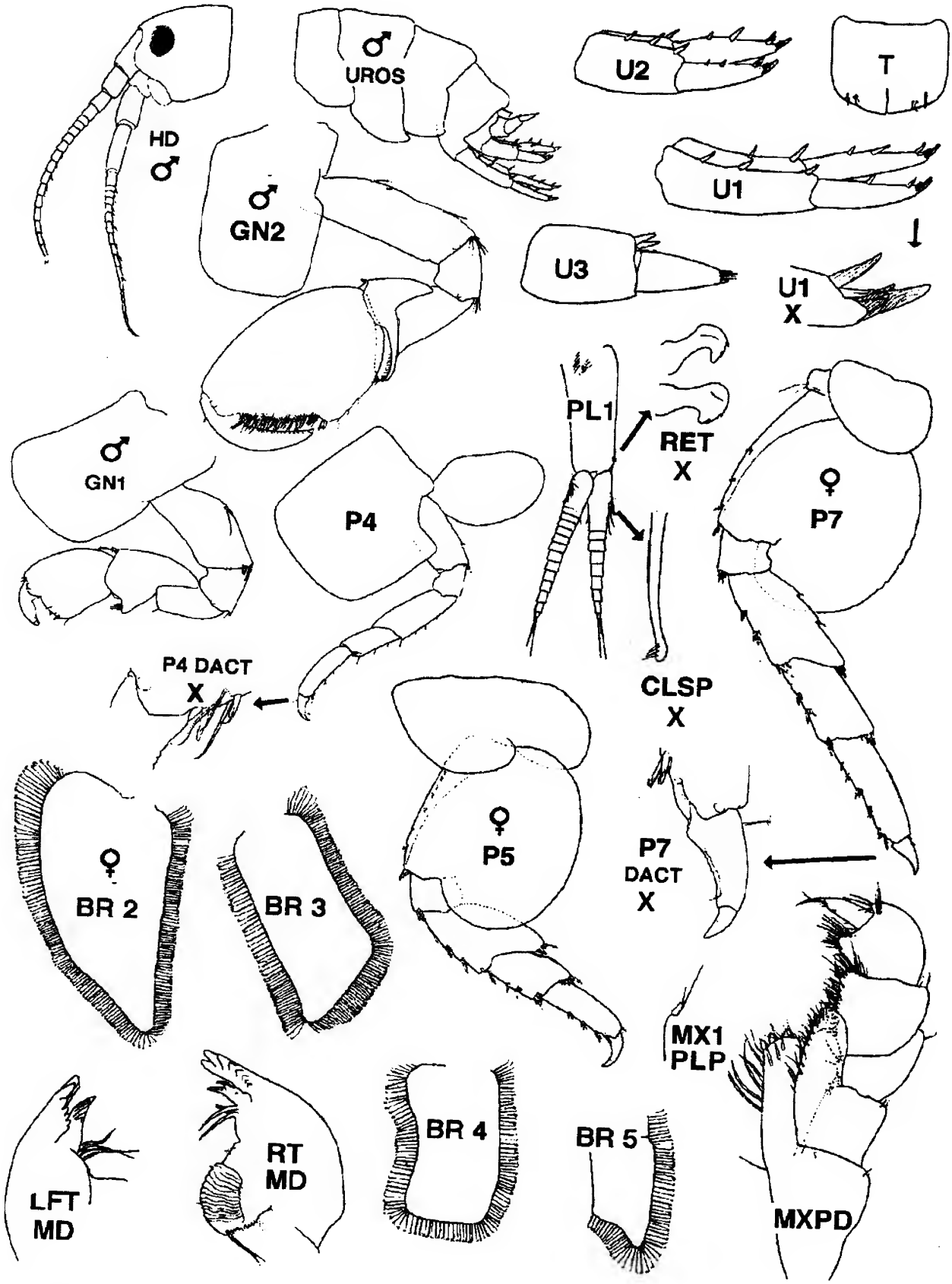


Fig. 10. *Allorchestes hirsuta* Ishimaru, 1995. Male (10.3 mm); female (10.0 mm). Southern Sea of Japan (after Ishimaru, 1995)

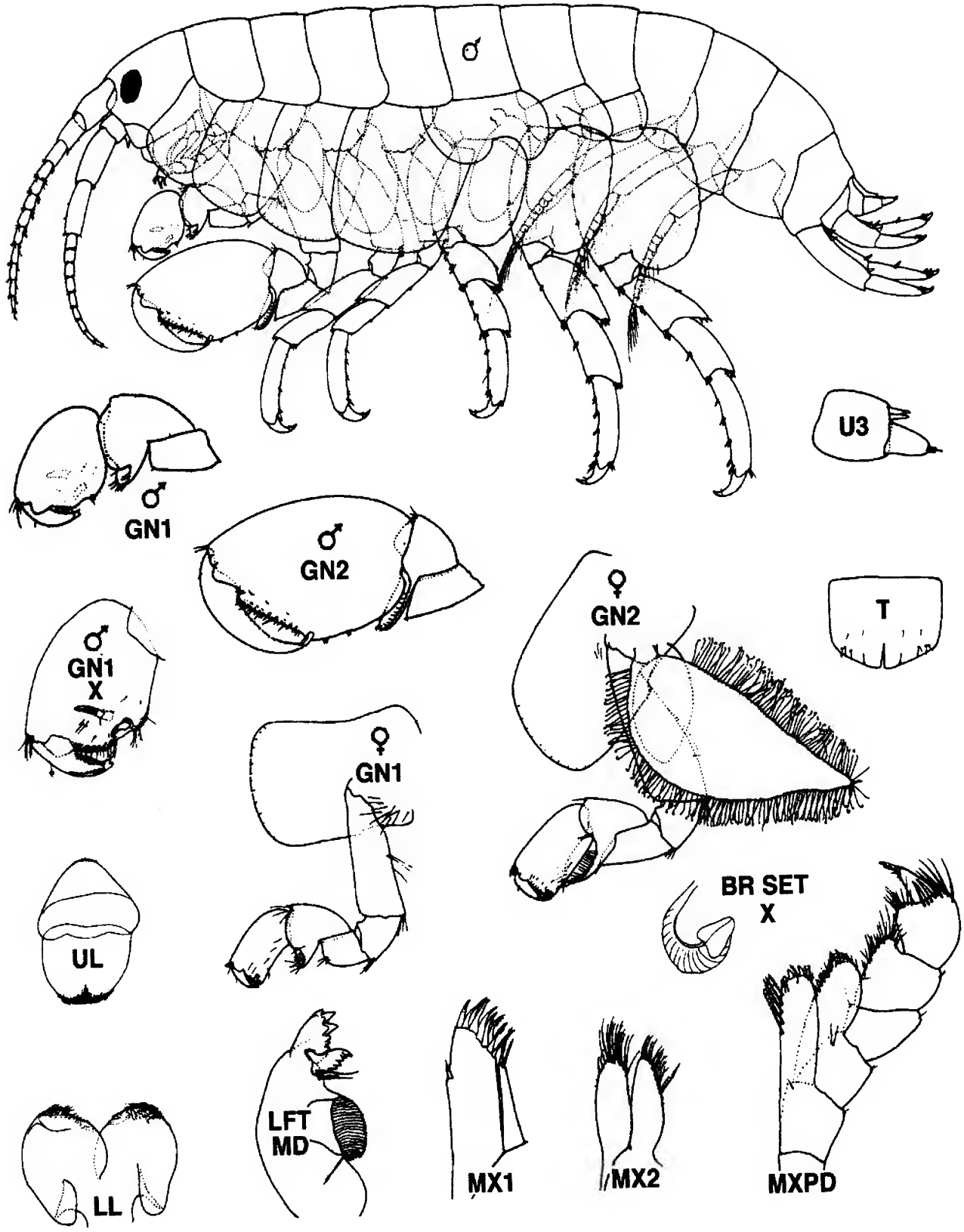


Fig. 11. *Allorchestes malleola* Stebbing 1899. Male (5.0 mm); female ov (4.5 mm). Shikotan, Kurile Islands, Okhotsk Sea

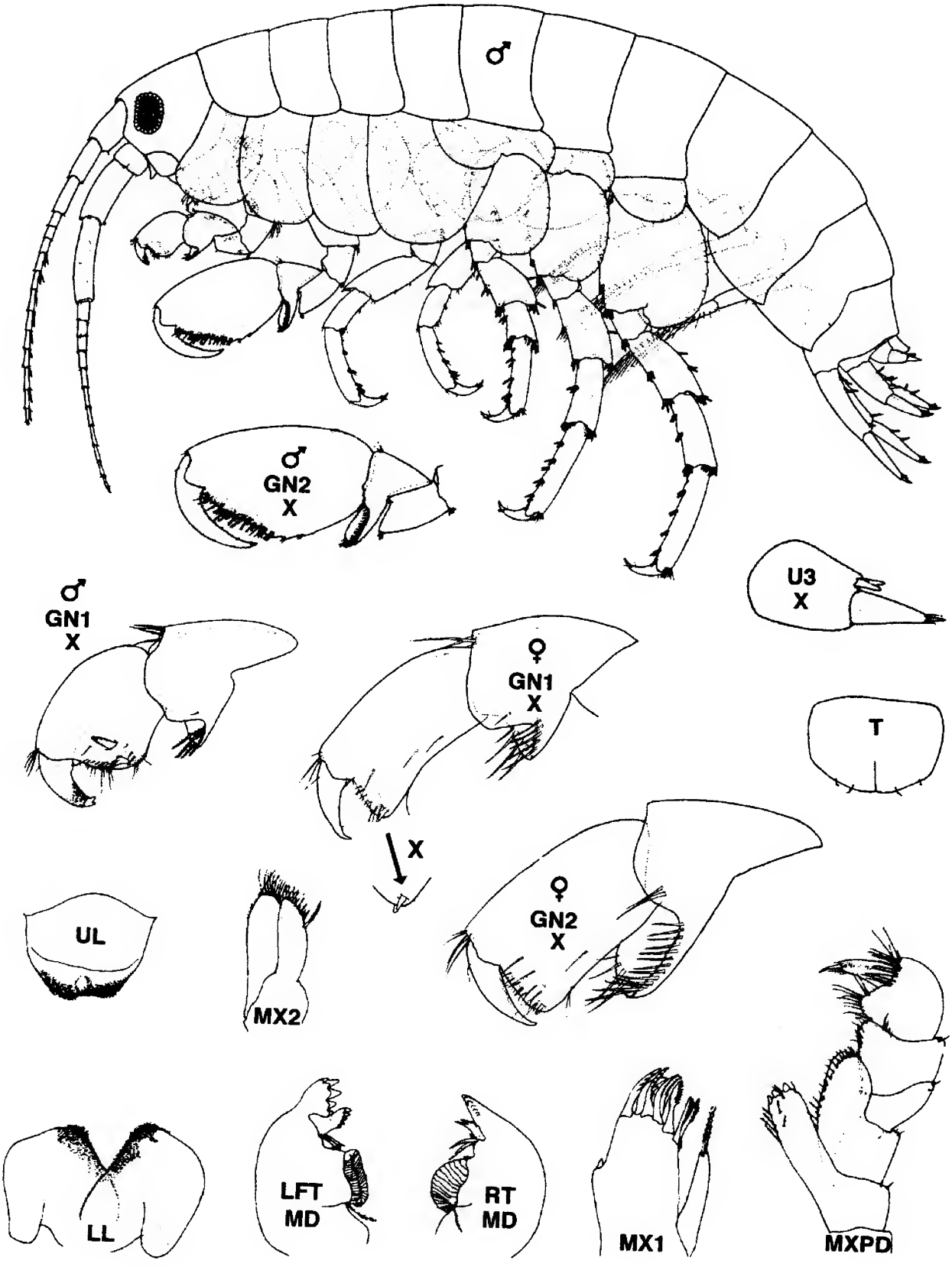


Fig. 12. *Allorchestes angusta* Dana. Male (5.2 mm); female (4.3 mm). Stn. P704, Amphitrite Point, Vancouver I., B. C.

examined, the synonymy is tentatively retained here.

Present study material of *A. malleola* Stebbing from Hokkaido, Japan, kindly supplied by Dr. A. Hiwatari, most closely resembles the individual parts figured by Bulycheva (1957) and is here considered to be that species. North American material from SE Alaska west to the Aleutian island chain has been identified as *A. angusta,* with character states trending to those of *A. malleola.* Thus pleopod peduncules of northern specimens tend to have 3 (rather than 2) retinacula.

However, material from the western Pacific identified and figured by earlier authors as *A. malleola* and *A. vladimiri* differs from *A. angusta* in the more slender form and positioning of amplexing spines of gnathopod 1 (male); the more rectangular form of coxae 2-4, the broader basis of peraeopod 7, the shorter blunter ramus of uropod 3, and the more obtuse angle of the pre-amplexing notch of the mature female (Fig. 6). Nagata (1965) also records a 9 mm male specimen from the Seto Inland Sea and an earlier record from Hokkaido both of which may may prove to be *A. malleola.*

Allorchestes angusta Dana
(Figs 1, 2, 3, 4, 5, 6h, 12)

Allorchestes angustus Dana, 1856: 177. Barnard 1952: 20-23, pl 5, figs. 2-6.
Allorchestes angusta Barnard 1974: 42; 1979: 91, figs. 50-52 (part). Bousfield 1981: 81, figs. 12, 13; 1996: 178, fig. 1.
non *Allorchestes angustus* Barnard 1954: 21-23. pl. 21 (= *A. bellabella).*
Allorchestes oculatus Stout, 1913: 651?

Material Examined: (About 600 specimens in 113 lots, SE Alaska to California. Numbers of specimens in parentheses).

Alaska:

Aleutian Islands: Stn 1A-2, Plot 32, Amchitka I., Alaska, C. E. O'Clair coll., 1974 - 6 subadult specimens (large dark reddish gray brown ring around eye).
Izenbak Lagoon, Unimak I., N. A. Powell coll., 1969 - 1 ♂ (slide mount), NMNS 69-319.

SE Alaska: ELB Stns., June-July, 1961: A2 (5); A7 (24); A8 94); A9 (5); A18 (6); A25 (1); A33, 2 lots (33 specimens - 1 slide mount); A57 (1); A86 (1); A88 (4); A92 (1); A99 (14); A114 (5); A105 (9); A115 (1); A121 (4); A131 (1); A136 (29) A140 (9); A153 (31). Dixon Harbor, K. E. Conlan coll., June 18/89 - 1 male (5.3 mm).

British Columbia:

Queen Charlotte Islands, ELB Stns. 1957: H5-2 lots (36); H8a (65 ♂♂ & ♀♀); H9 (1); W3a-2 lots (4); W5 (1); W15 - 2 lots (2).

North Central coast, ELB Stns., 1964: H1, West Beach, Calvert I., July, 2 lots - 2 ♂♂, 2♀♀; H5 (2); H6 (2) H7 (2); H10 (3); H11(25); H12 (9); H18 (2); H23 (4); H26 (1); H29 (1); H35 (1); H40 (6); H44 (14); H48 (20); H57 (7). ELB Stn. P14, Porpoise Harbour, June, 1961 - 31 ♂♂, ♀♀.

South Central Coast, ELB Stns., 1955: M1 -Savary I. (8); M3 (6); M5 (27); M11 - White Rock (11).

Northern Vancouver Island, ELB Stns., July-Aug., 1959: N13 (2); O1 (2); O2a (9); O6 (1 ♂♂, 2 ♀♀ - 1 slide mount); V4b (1); V11 (1); V19, 2 lots (25); V27, 2 lots (4).

Southern Vancouver I., ELB Stns., July, 1955:
F4a (2); F6 (5); G2 (28); G10, 2 lots (58); G13, Piper's Lagoon, 2 lots - 54 ♂♂, ♀♀; P2 (1); G11a, SE End Wickininnish Bay - 1♂ (slide mount). ELB Stn. H44, Brady's Beach, July 1964 - 1 ♂ (slide mt).
ELB Stns., July , 1970: P704, Amphitrite Point - 29 specimens incl. 1 ♂ (5.2 mm); 1 ♀ (4.3 mm), (fig'd specimens); P705 (14); P708 (107 ♂♂, ♀♀); P717 (1).
ELB Stns., May, 1975: P1c (4); P13 (40); P19a (5); P25 (1).
ELB Stns., May, 1976: B3 (1); B4 (1).
ELB Stns., May, 1977: B5 (4); B6b, 2 lots (6); B16 (10).

Other B.C. material: Anthony I., Queen Charlotte Ids., G. C. Carl coll., 1956 - 1♀; Stn. 13, Gulf Islands, D. Kittle coll., 1972 - 50 ♂♂, ♀♀; Parry Bay, near Weirs Beach, KDH coll., 1974 - 4 juveniles, BCPM 974-182-8; Stn. 6, Chemainus estuary, D.V. Ellis coll., 1976 - 1 ♂; Juene Landing, R. Coates coll., 1976, 2 lots - 2 specimens (slide mounts), RBCM Nos. 980-486; Salmon R. estuary, Vancouver I., R. Coates coll., 1976, 2 lots - 17 ♂♂, ♀♀ (slide mount), RBCM No. 977-471-8; Ibid - 33.

Wash.-Oregon, ELB Stns., July-Aug., 1966: W4 (9); W5 (10; W7 (1); W8 (30); W16 (10); W28 (1); W30, 2 lots (17); W39 , 2 lots (7).

California: ELB Stn. C3, Baker's Beach, San Francisco, July, 1959 - 1 juv.; Pt. Loma, San Diego, W. Klawe coll., 1956 - 2 ♂♂; Mission Bay, San Diego, W. D. Clarke coll., 1956 - 1 ♂

Mexico: Turtle Bay, B. C., W. Klawe coll., 1956 - 1 ♂.

Diagnosis: Male (5.2 mm; to 7 mm - Barnard 1979).

Body small to medium, mid-dorsally on urosome smooth. Head regular. Eyes medium large, broadly subreniform, black. Antennae medium. Antenna 1, flagellum 11-12 segmented. Antenna 2, flagellum 11-13-segmented, distal segments slender.

Mandible: left lacinia 5-dentate; left and right spine rows with 2 blades. Maxilla 1, palp small. Maxilla 2, inner plate regular, marginal plumose seta strong. Maxilliped, inner plate with oblique apex; outer plate medium; palp segments 2 & 3 broad, massive, dactyl slender, unguis short.

Coxal plates 1-3 each with slight posterior marginal cusp, lower margins sub-truncate Coxa 4 as broad as deep, lower margin convex. Coxa 5 shallow, aequilobate. Coxal gills medium large, sac-like, small-

est on peraeopod 2.

Gnathopod 1, carpal lobe lined with 9-10 medium finely pectinate comb setae; propod medium deep, broadening distally to slightly oblique palm that is convex medially; guiding spine short, thick, apically striated, set vertically to palm; dactyl short, moderately thickened proximally, unguis asymmetrically bifid, closing on locking spine. Gnathopod 2, carpal lobe large, with 24 closely set marginal comb-setae; propod, posterior margin medium long, palm nearly straight, lined with longish spines; inner margin of dactyl lined with 16 spinules .

Peraeopods 3 - 4, posterior margin of segment 6 with 4-5 single small spines. Peraeopods 5-7, bases relatively shallow, deeper than broad; segments 4-6 little broadened, posterodistal margins and apices with pairs or small clusters of simple spines.

Epimeral plates 2 & 3, hind corners sligthly produced, acute. Pleopod peduncles each with 2 retinacula. Uropods 1 & 2, marginal spines lacking on outer ramus and distally on peduncle of uropod 1. Uropod 3, peduncle short, with 1-2 apical spines; ramus slender, tapering to subacute apex bearing a spine and 2-3 short setae.

Telson squarish, lobes narrowly cleft 1/3 to base.

Female ov (4.5 mm): Coxal plates 2-4 large, deep; coxa 4 deeper than broad. Peraeon segment 2, preamplexing notch medium shallow, located nearly at mid point of lower margin; notch angle obtuse (~125°); locking slit positioned closely dorsad; unguisial groove lacking

Gnathopod 1, carpal lobe medium, distally with longish comb spines; propod medium deep, length subequal to carpus, palm gently convex, nearly transverse. Gnathopod 2, carpal lobe large, deep, with numerous medium comb-spines; propod medium deep, palm slightly oblique.

Brood plates medium large, margins with numerous short fine hooked setae.

Distributional Ecology. Small specimens (males to 7 mm) occur from S. California north to British Columbia. Slightly larger animals (8-9.3 mm) from SE Alaska and the Aleutian chain trend toward the character states of, but remain distinct from, those of *A. malleola* of the western Pacific. According to Barnard (1979), the species is phycophilous and mainly intertidal, rarely subtidal.

Remarks: Barnard (1979) has synonymized the western Pacific material from Japan and USSR with the N. American *A. angusta*. Dana's type is from California so that *A. malleolus* and *A. vladimiri* would be junior synonyms. However, taxonomic evidence for the distinctness of *A. angusta* includes the different form of the preamplexing notch of the female, as described .

Barnard (1979) and Barnard & Karaman (1991) have included *Allorchestes oculatus* Stout, 1913, from Laguna Beach, southern California, in the synonymy of *A. angusta* Dana. Stout's unillustrated original description of the mature male of *A. oculatus* detailed its colour in life, and the large size of the eyes that nearly meet mid-dorsally. The brief outline otherwise provided little taxonomically useful information. Though Dr. Barnard apparently examined fresh material from south of Pt. Conception, such conspecificity would seem unlikely. Thus, the range of well-illustrated material of *A. angusta* extends from Central California, dominantly through British Columbia, to Alaska, yet very few inshore inverbrates occur both in the Bering Sea (Alaskan Aleutian Chain) and in southern California, south of Pt. Conception.

For the present study, CMN collections contain a single 5.0 mm male specimen of *Allorchestes* sp. from Mission Bay, San Diego, collected by C. D. Clarke, June, 1956. Examination of the slide-mounted appendages revealed several differences from northern specimens of *A. angusta* of slightly larger size (Fig. 12). Especially noticeable in the San Diego specimen were: (1) the relatively large eyes; (2) the relatively short antennal flagella; (3) the relatively short palmar margin of the propod of gnathopod 1; (4) the elongate ischium, and small, weakly spinose propod of gnathopd 2; (5) the squarish coxa 4; (6) the relatively large and deep posterior lobes of coxae 5 & 6; and (7) the relatively short propods (segment 6) of peraeopods 5-7. However, the limited nature of this material, lacking females and comparative series of specimens, renders the nature of these differences inconclusive. The authors therefore tentatively follow Barnard's synonymy of *Allorchestes oculatus* within *A. angusta,* pending further careful study of extensive regional material.

Allorchestes rickeri n. sp.

(Figs. 2, 3, 4, 5, 6i, **13**)

Allorchestes parva Bousfield, 1981 (nomen nudum): 81 , figs 12, 13.—Bousfield 2001: 104.

Material Examined: Approx. 135 ♂♂, 155 ♀♀, 20 juv., in 41 lots, Northern B. C. to California. Number of specimens in parentheses).

Alaska:
S.E.Alaska: ELB Stns., June-July, 1961: A22 (1), A80 (42 ♂♂, ♀♀) , A140 (3).
British Columbia:
Queen Charlotte Islands, ELB Stns., 1957: W1 (2); W8 (2); W11 (8); W12 (2).
North Central Mainland, ELB Stns., July, 1964: H23 (18; H41 (18); H50 (3).
North Vancouver I., ELB Stns., July, 1959: V27 (1).
South Vancouver I. ELB Stns., July-August, 1955: P6a, South end Wickaninnish Bay - 81 ♂♂, ♀♀ (slide mount); P6e (2). ELB Stns., July, 1970: P708, 2 lots (15); P714, Clo-oose, 2 lots - ~350 ♂♂, ♀♀. ELB Stns., May, 1975: P14b (9). ELB Stns., May, 1977: B6b (2 ♂♂); B11a (6), 2 lots (35); B12b (2); B19b (10).
Other B. C. material: Pachena Bay, 20 ft. sand, P. Slattery & C. Oliver coll., Apr. 17/83 - 42 ♂♂, 52♀♀, 20 juv. (slide mounts); Port Louis, EAH coll., Jan 20/90 - ♂, ♀ (mating pair).
Wash.-Oregon, ELB Stns., July-Aug., 1966: W8 (1); W18, ♂ (3.0 mm); ♀ ov (3.0 mm); W22, 2 lots (3); W33 (1); W34 (6); W35 (1); W36 (7); W40 (2); W46 (4); W57 (1); W61, Neskowin Beach, Low intertidal -1 ♂ (3.0 mm) (slide mount), **Holotype**, CMNC 2001-0028; ♀ ov (3.0 mm)(slide mount), **Allotype**, CMNC 2001-0029; 2♂♂, 2 ♀♀, **Paratypes,** CMN Nos.2001-0030; lot No. 2 - ~250 ♂♂, ♀♀ Topotypes. W63 (1).
California: Stn 89-1-3, Spanish Bay, Monterey peninsula, K.E.Conlan coll., Jan. 2/89 - 1 ♂ (5.8 mm), 1 ♀.

Diagnosis: Male (3.0 mm): Body small, mid-dorsally smooth. Head regular. Eye medium, broadly sub-reniform, black. Antennae short. Antenna 1, flagellum 9-segmented. Antenna 2, flagellum 9-segmented, distal segments slender.

Mandible: left lacinia 6-dentate; spine rows with 3-4 blades. Maxilla 1, palp small. Maxilla 2, inner plate regular, marginal plumose seta strong. Maxilliped, inner plate with oblique apex; outer plate medium; palp segments 2 & 3 medium broad, dactyl longish, slender.

Coxal plates 1-3 with very weak posterior marginal cusp, lower margins very shallowly rounded. Coxa 4 large, nearly as broad as deep, lower margin evenly convex. Coxa 5 shallow, aequilobate.

Gnathopod 1, carpus deep; propod medium deep, broadening distally to a short convex palm, guiding spine short, striated, set at angle to palm; dactyl thickened basally, unguis unequally bifid, closing on short, thick locking spine. Gnathopod 2, carpal lobe short, with short marginal comb-setae; propod, posterior margin relatively short, distally straight; palm nearly straight, lined with short spines.

Peraeopods 3 - 4, posterior margin of segment 6 with 2-3 groups of small complex spines. Peraeopods 5-7, bases broad, rounded; segments 4-6 broaded, posterodistal margin and apices with cluster of short simple spines.

Epimeral plates 2 & 3, hind corners nearly square. Uropod 1, peduncle with proximal outer marginal spines only, distally bare; outer ramus lacking marginal spines. Uropod 3, peduncle thick, with 2 distal spines; ramus shorter, slender, tapering to short-setose apex.

Telson subrectangular, lobes narrowly cleft 1/4.

Female ov (3.0 mm): Peraeon segment 2 (Fig. 6), preamplexing notch medium, located anteriorly on lower margin; notch angle steep, slightly obtuse (~105°); locking slit positioned posteriorly dorsad; unguisial groove lacking; posterior lobe relatively shallow.

Gnathopod 1, carpal lobe medium distally with longish comb spines; propod medium deep, length subequal to carpus, palm gently convex, vertical. Gnathopod 2, carpal lobe large, deep, with numerous medium comb spines; propod medium shallow, palm slightly parachelate.

Brood plates medium large, margins with numerous short fine hooked setae.

Etymology: The patronym recognizes the outstanding career contributions of the late W. E. Ricker to the aquatic biological and fisheries sciences of North America.

Remarks: In nearly all character states, *Allorchestes rickeri* is clearly a member of the *angusta* group. However, it is distinctive in the relatively large coxal plates 1-4 , shallow propod of gnathopod 1 (male); short, broadened segments 4 & 5 of peraeopods 5-7 and the parachelate gnathopod 2, and relatively sharply angled pre-amplexing notch in the female.

Hyalella Smith

Hyalella S. I. Smith, 1874: 645. Stebbing 1906: 574. Bulycheva 1957: 181. Barnard & Barnard 1983: 708. Bousfield 1996:183; 2001:104. Witt & Hebert 2000: 687.

Type species: *Amphithoe azteca* Saussure, 1858.

Species (North America): *Hyalella (Hyalella) azteca* (Saussure, 1858); *H. (H.) inermis* Smith, 1874; *H. (H.) longicornis* Bousfield, 1996; *H. (H.) muerta* Baldinger, Shepard, & Threloff, 2000; *(H.) montezuma* Cole & Watkins, 1977; *H. (H.) sandra* Baldinger, Shepard, &

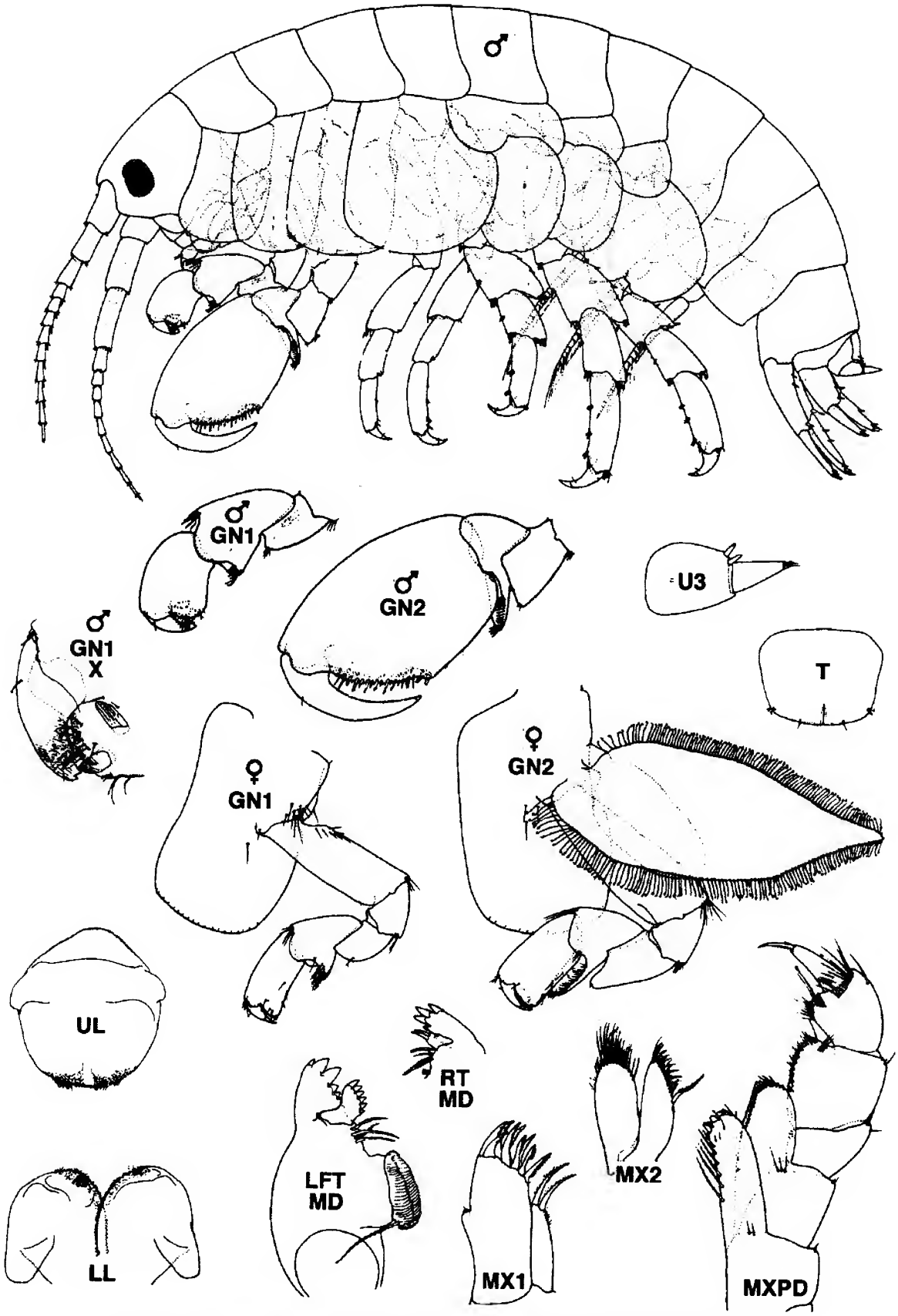


Fig. 13. ***Allorchestes rickeri*, n. sp.** Male (3.0 mm); female ov (3.0 mm). Stn. W61, Neskowin Beach, Oregon. Low intertidal.

Threloff, 2000; *H. (H.) texana* Stevenson & Peden, 1973.

Diagnosis: Body smooth, mucronate, or processiferous. Antennae short to medium. Antenna 2 (male), peduncular segments regular, not stoutly expanded; flagellar segments not incrassate (conjoint); gland cone large, prominent.

Mouthparts regular. Mandible: molars with distal plumose seta; left lacinia 5-dentate. Maxilla 1, palp small, 1-segmented. Maxilliped, palp unguiform, dactyl without whip.

Coxal plates 1-4 deep, subquadrate, lacking posterior marginal cusps. Coxae 5 & 6 posterolobate. Gnathopods strongly sexually dimorphic; gnathopod 1, dactyl basally stout, unguis simple; propodal postero-distal spines unmodified. Gnathopod 2 (male) propod large, palm oblique. Peraeopods 3-7 slender, spines simple; dactyls simple. Coxal gills large, sac-like, subequal. Paired sternal gills ventrally on peraeon segments (2) 3-7.

Pleopod peduncles with 2 retinacula. Uropods 1 & 2, rami marginally spinose. Uropod 3 uniramous; ramus slender, apex with slender spines.

Telson entire; lobes fused apically.

Female: Peraeon segment 2, pre-amplexing notch regular, simple. Gnathopod 1 regularly subchelate, propod shorter than carpus. Gnathopod 2 subchelate to parachelate; propod longer than carpus.

Brood plates relatively short and broad, marginal setae short to medium.

Hyalella azteca (Saussure)
(Figs. 4, 5, 6a, **14**)

Hyalella (H.) azteca Bousfield 1996: 183 (and synonymies).

Material Examined:
SE Alaska: ELB Stns, June-July, 1961: A166, Leo Anchorage, at Anclote stream, July 29 - 1 ♂ (4.5 mm); 1 ♀ ov (4.0 mm) (**fig'd specimens**), CMN colIns.
British Columbia:
South Vancouver I: Horsefall, Departure Bay. Vancouver I., Lot No 51, JFL Hart coll., July 6/33 -1 ♀. ov (4.0 mm)
Wash.-Oregon: ELB Stns., July-Aug., 1966: W23, Lake Quisiault, at Falls Creek, July 22 - ~30 ♂♂ &♀♀ specimens (4-4.5 mm); W27, Lake Crescent, July 24 - 2 ♀♀ (4.7 mm), 4 juveniles, CMN colls.
Other U.S. material: Lake Leota, King Co., in *Utricularia* bladders, R. Wallace coll. - 1 ♀ (2.5 mm). Warm Springs, near Frenchglen, Herney Co., (42°48'N., 118°54'N), in spring 1280 m a.s.l., G. W. Courtney coll., July 7/87 - 6 ♂♂, 6 ♀♀ (3.5 - 3.8 mm); CMN colIns.
California: Malibu Lagoon State Park, D. Galli coll., Jan. 25/84 - 1 ♂ (5.0 mm); CMN colIns. IZ 1984-39.

Distributional Ecology (Pacific drainages): Fresh and slightly brackish waters of lakes rivers and upper tidal portions of estuaries, Mexico and California north approximately to the tree line of Alaska.

Remarks: The small mature male and female specimens from springs at Frenchglen are quadrimucronate, having postero-dorsal mucronations on peraeon segment 7 and all three pleon segments.

Parhyalella Kunkel
(see Figs. 6d, **15**)

Parhyalella Kunkel, 1910: 74. Bulycheva 1957: 181. Barnard & Karaman 1991: 372. Bousfield 1996: 182. Lazo-Wasem & Gable 2001: 5.
non *Parhyalella* Krapp-Schickel 1993 (= *Marinohyalella*).
non *Exhyalella* Stebbing, 1917 (Type-*E. natalensis*)

Type species: *Parhyalella batesoni* Kunkel, 1910, monotypy.

Species: *Parhyalella barnardi* Lazo-Wasem & Gable, 2001 (Baja California); *P. congoensis* Ruffo, 1953 (SE Atlantic); *P. kunkeli* Lazo-Wasem & Gable, 2001 (Taiwan); *P. nisbatae* Lazo-Wasem & Gable, 2001 (Caribbean); *P. pietschmanni* Schellenberg, 1938 (Hawaii); *P. ruffoi*, Lazo-Wasem & Gable, 2001; *P. steelei* Lazo-Wasem & Gable, 2001; *P. whelpleyi* (Shoemaker, 1933) (Caribbean to Brazil); *Parhyalella* spp. Lazo-Wasem & Gable, 2001 (Bahama Ids., Cuba, Florida Keys to US coast of Gulf of Mexico; also S. Korea).

Diagnosis: Antennae variable, mostly short. Antenna 2 (male), peduncle very stout; basal flagellar segments conjoint; gland cone small.

Mandibular left lacinia 5 1/-2-dentate; molar seta lacking. Maxilla 1 lacking palp. Maxilliped palp, dactyl unguiform, without whip.

Coxae 1-4 lacking posterior marginal process. Gnathopods strongly sexually dimorphic. Gnathopod 1 (male), dactyl often bifid medially; gnathopod 2 (male) propod large, palm setose or spinose, carpal lobe distinct. Peraeopods slender, homopodous, weakly spinose; dactyls medium, without medial spine. Coxal gills medium, sac-like, subsimilar. Sternal gills lacking.

Uropod 1, peduncular spines ordinary; rami margin-

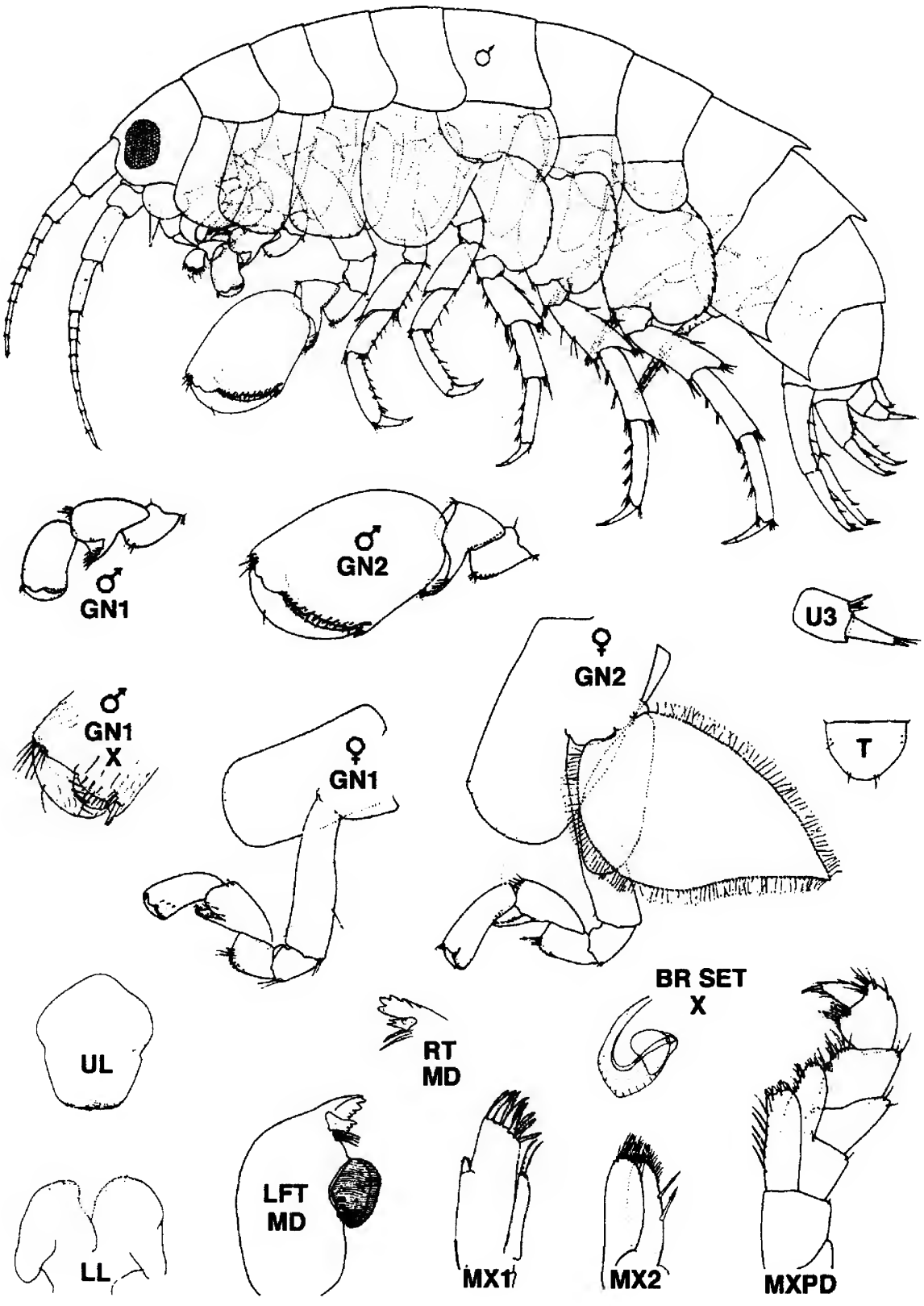


Fig. 14. *Hyalella azteca* Saussure, 1858. Male (4.5 mm); female ov (4.0 mm). ELB Stn. A166, Leo Anchorage, at Anclote stream, SE Alaska.

ally spinose. Uropod 3, peduncle relatively slender, ramus short, apex with slender spines.

Telson plate-like, entire.

Female: Peraeon segment 2, preamplexing notch ordinary, lacking locking slit and unguisial groove. Brood plates slender, apex acute; marginal setae medium short.

Distributional Ecology: Low intertidal and shallow waters of protected coasts and estuaries, often associated with *Enteromorpha* in brackish pools and seeps. Along tropical and warm-temperate shores of Pacific, Atlantic and Indian Oceans, south to Central Chile, and north to Ensenada, B. C., Mexico.

Remarks: The type locality of *Parhyalella barnardi* is Ensenada, Baja California, Mexico, very close to the southern limit of the present study region.

Parhyalella steelei Lazo-Wasem & Gable
(Fig. 6d)

Parhyalella steelei Lazo-Wasem & Gable, 2001: 37, figs. 28-31.
Parhyalella pietschmanni Steele, 1973: 276, figs. 1-4.

Material Examined:
Ambatoloaka, Nosy Bé, Madagascar, in drifting dead turtle grass, D. Steele coll., July - December, 1963. - numerous ♂♂ ♀♀, and imm. specimens, CMN collns.

Remarks: Steele (1973) detailed the life history of a species of *Parhyalella,* recently described as *P. steelei* Lazo-Wasem & Gable, that occurs commonly at Nosy Bé, Madagascar. He noted that the pre-amplexing male utilized gnathopod 1 in grasping the female about the level of peraeon segment 2.

The preamplexing notch of a female specimen from the original material is illustrated in Fig. 6d. Its form in other species of the genus, and in *Exhyalella* and *Marinohyalella* remains to be fully described.

Parhyalella sp.
(Fig. 15)

Parhyalella whelpleyi Bousfield 1996: 181, fig. 2.
Parhyalella sp. Lazo-Wasem & Gable 2001: 43?

Material Examined: Isla Arenas, Cuba, sandy shore, LW. - ♂ (7.5 mm); ♀ (5.5 mm) (slide mounts), CMN collns.

Remarks: Bousfield (1996) figured material from Isla Arenas, Cuba, as *Parhyalella whelpleyi* Shoemaker, 1933. This figure, partly reproduced here (fig. 15), differs in several respects from the more detailed figures and description of *P. whelpleyi* provided by Lazo-Wasem and Gable (2001). The present species may be similar to, or perhaps identical with, undescribed species recorded by those authors from the Florida Keys, in GCRL collections from along the Gulf coast of Alabama and Mississippi (LeCroy, pers. comm.), and in unidentified CMN collections of *Parhyalella* from the Bahamas, Florida, and the Gulf coast.

DISCUSSION

Phyletic Relationships

Family Hyalellidae has long been considered an integral part of, or closely related to, family Hyalidae (Stebbing 1906; Bulycheva 1957; Barnard & Karaman 1991; Bousfield 1996). In a recent analysis of genus *Parhyalella*, Laso-Wasem & Gable (2001) revived genus *Exhyalella* Stebbing,1917, created the monotypic genus *Marinohyalella* for *P. richardi* Chevreux, 1902 of the Mediterraean region, but retained all three genera with family Hyalidae (sens. lat.).

Fig. 16 portrays character state similarities of world genera and subgeneric groupings utilized here within family Hyalellidae. The analytical treatment employs a semi-phyletic modification of the UPGMA system of Sneath and Sokal (1973), as in previous analyses of other North Pacific amphipod taxa. Character states are ordered plesio-apomorphically and the relative phyletic placement of a given taxon is represented by a numerical sum of plesiomorphic, intermediate, and apomorphic character state values (0, 1, and 2, respectively) in a Plesio-Apomorphic (P.-A.) Index. The matrix of 12 characters and corresponding character states on which the resulting phenogram is based are mainly those of Lazo-Wasem & Gable (2001), and may be supplied on request.

The phenogram reveals two major generic subgroupings at and above the 50% similarity level: a relatively primitive assemblage of genera and subgroups on the left (P.-A. index 5-10), and an advanced generic group on the right (P. A. Index 11-13). The former embraces the North and South Pacific genus *Allorchestes*, the very closely related Mediterranean genus *Marinohyalella* (~80% similarity), and the large and diverse, but less closely similar, neotropical freshwater genus *Hyalella*. The advanced tropical and

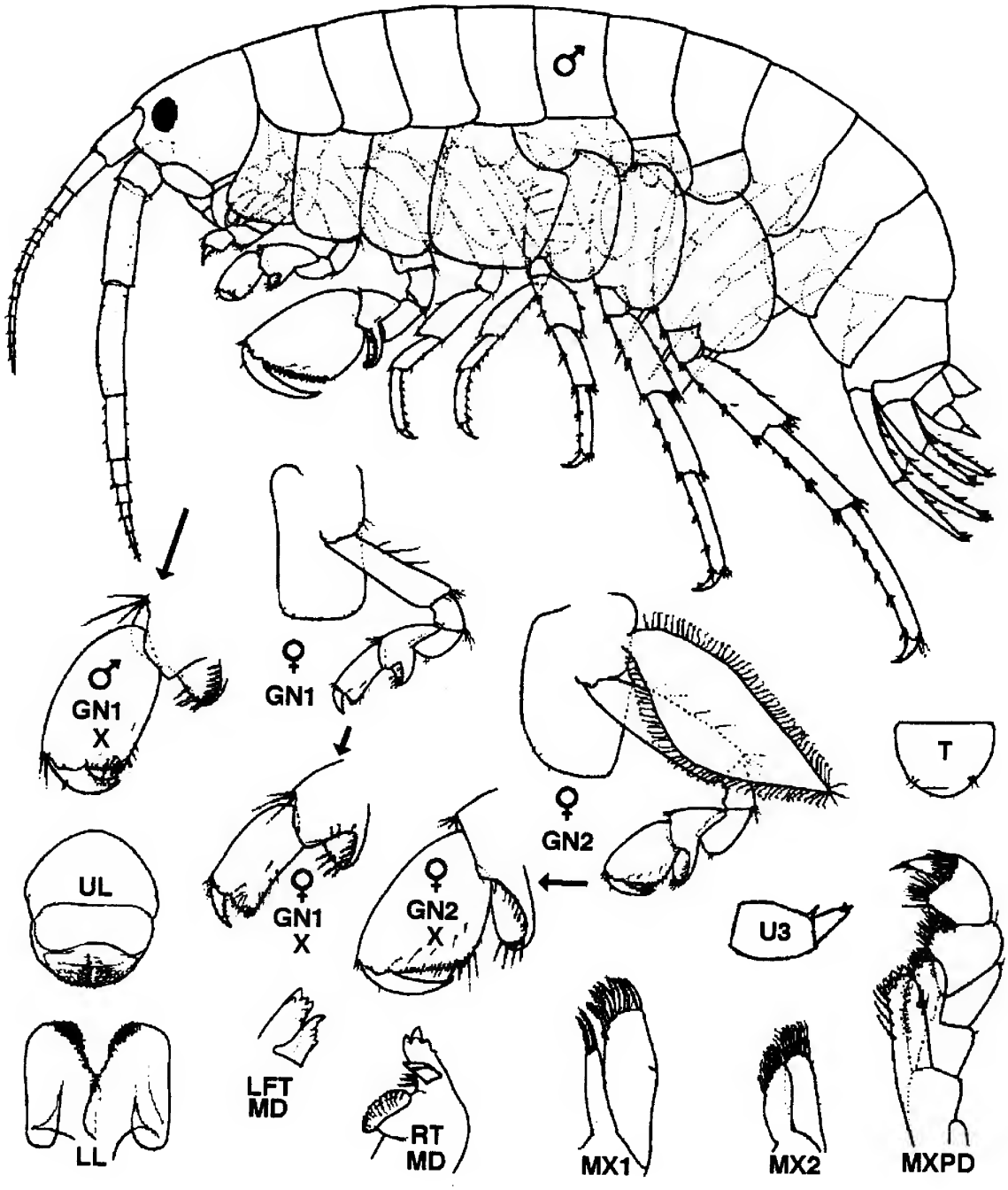


Fig. 15. *Parhyalella* sp. Male (7.5 mm); female (5.5 mm). Sandy shore, LW. Isla Arenas, Cuba.

warm-temperate marine genera *Exhyalella,* and the *Parhyalella* complex, cluster at only the 65% level of similarity, in our viewing justifying the recent decision of Laso-Wasem & Gable (2001) to separate the two genera. The relatively close morphological similarity of *Marinohyalella* to both *Allorchestes* and *Hyalella,* and its former inclusion within genus *Parhyalella,* tends to support the placement of all five genera within family Hyalellidae as here defined.

Using a broader set of species level characters, Fig. 17 portrays character state similarities within known species and subspecies of genus *Allorchestes* in relation to outgroup genera *Parhyalella* and *Hyalella.* Characters and character states on which the resulting phenogram is based are given in Table I. Cluster analysis data on which the phenogram is based are considered overly bulky and repetitive for publication here, but may be supplied on request.

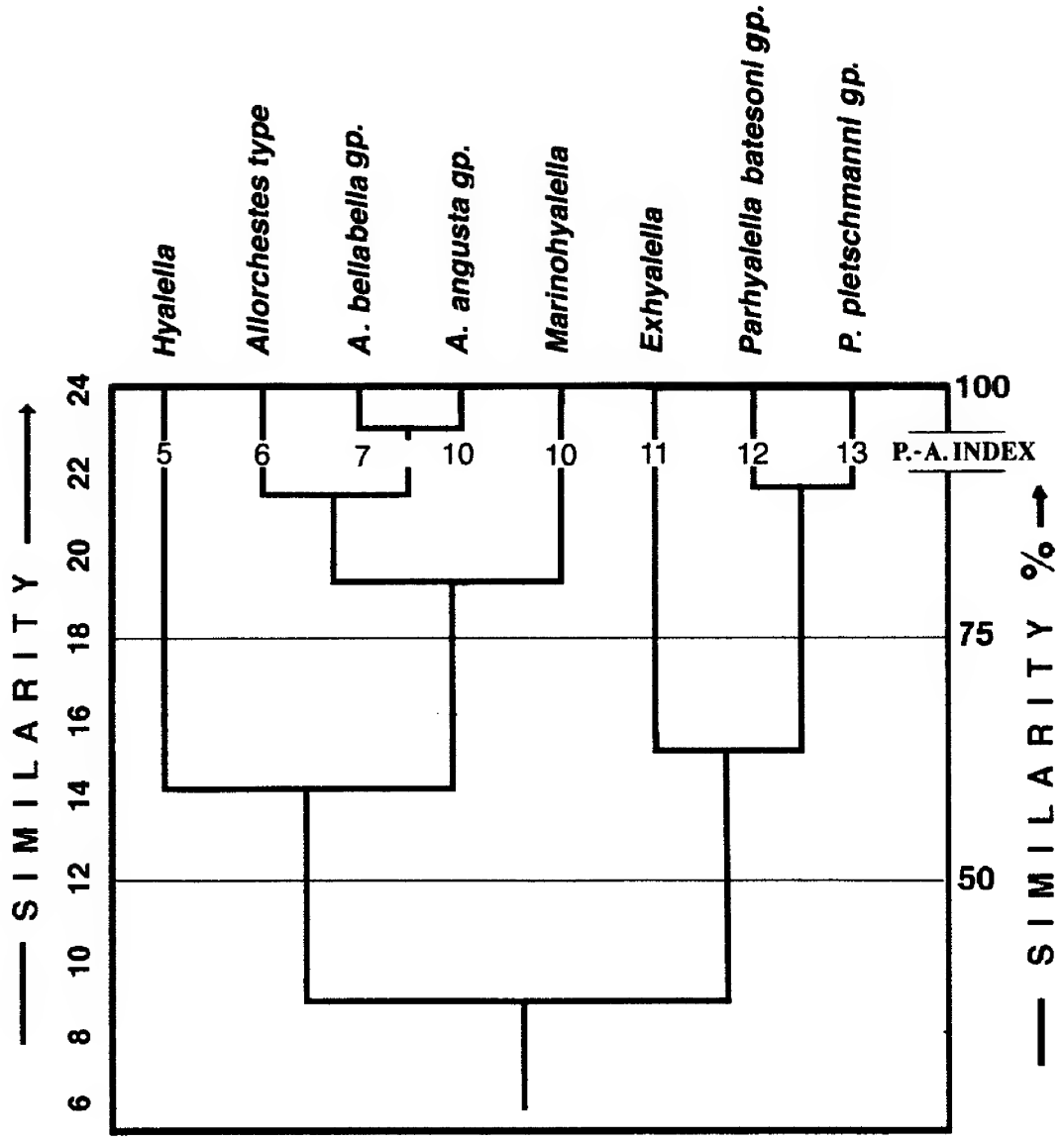


Fig. 16. Phenogram of morphological similarities of genera and species groups within family Hyalellidae

Two major subgroups of *Allorchestes* are discernible above the 50% similarity level: a relative primitive (P.-A. index 10-18) assemblage of species from the southern hemisphere, and three large species from the northernmost North Pacific region. These all share a simple-tipped dactyl of gnathopod 1 (male), normally spinose peduncle of uropod 1, and squarish, often deeply cleft telson. To the right is a cluster of 4 more advanced species (P.-A. indices of 19-29) that share a split-tipped unguis of the dactyl of gnathopd 1 (male) as well as a disruptively spinose peduncle of uropod 1, and a broadly rectangular, shallowly cleft telson. Within the primitive subgroup, *A. bella bella* and *A. priceae* are closely similar in the relatively elongate antennal flagella, the swollen condition of the dactyl of gnathopod 1 (male), and the ventrally rounded coxae 2-4.

Within the advanced *angusta* subgroup, *A. hirsuta* is a relatively primitive western Pacific member. Close similarity of the Asiatic *A. malleola* and the North American *A. angusta* is here confirmed, but differences, especially in their preamplexing morphologies, are deemed sufficiently great to justify resurrections of these two forms as distinct species. *Allorchestes rickeri* is a North American-endemic member of the *angusta* complex, occuring mainly on shallow sandy substrata, that is especially distinctive in the form of its preamplexing morphology, in both males and females.

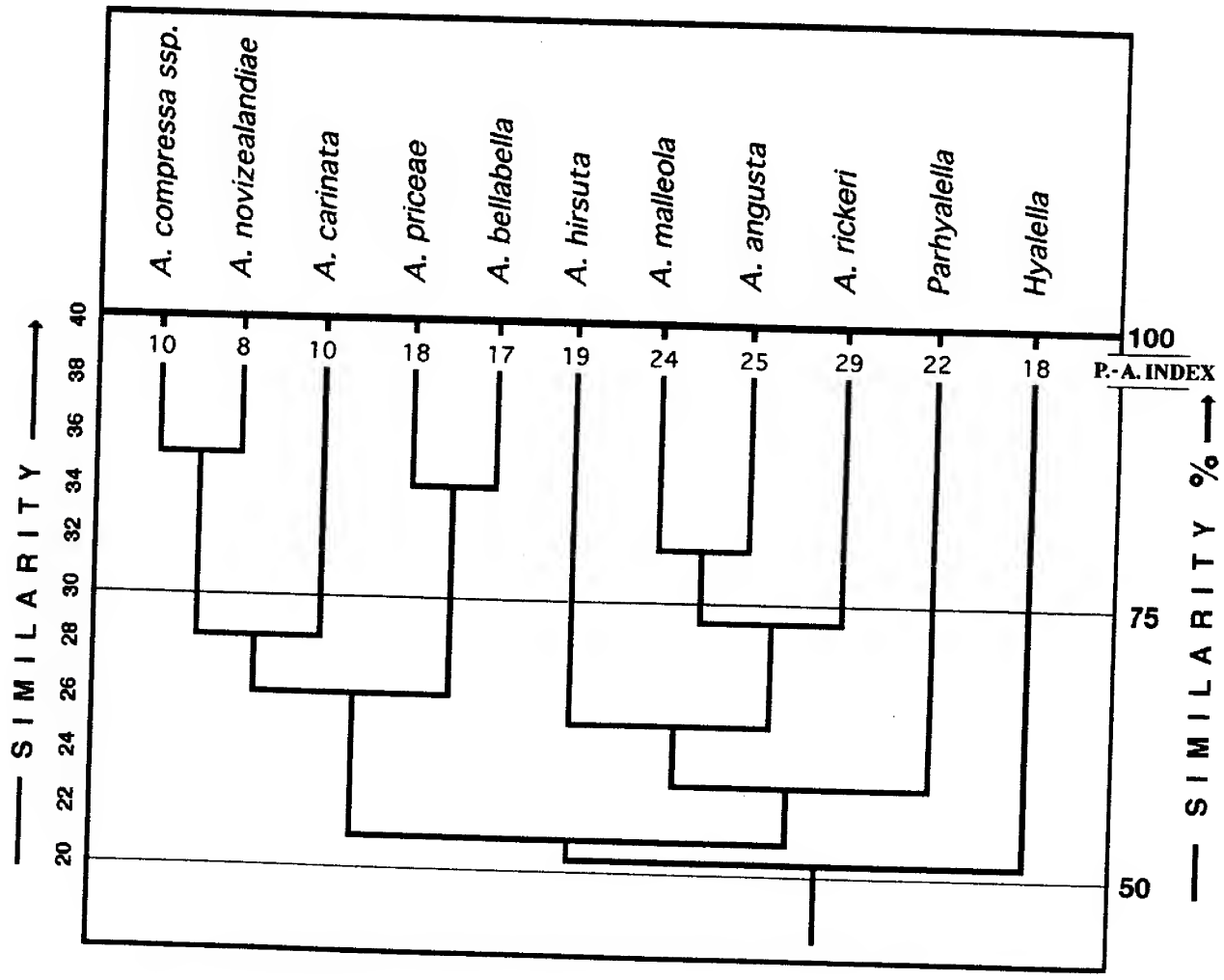


Fig. 17. Phenogram of morphological smilarities and possible phyletic relationships among species of *Allorchestes*; in relation to *Parhyalella* and *Hyalella* outgroup genera.

Biogeography of North Pacific Hyalellidae

The distribution in the North Pacific Rim region of 7 species of *Allorchestes*, northern records of the tropical-warm temperate genus *Parhyalella*, and North American records of the neotropical freshwater genus *Hyalella* are summarized semi-diagramatically in Fig. 18. With respect to the cold-temperate genus *Allorchestes*. *A. hirsuta* and *A. malleola* occur in the Western Pacific region only (Zone 1). Three species, *Allorchestes priceae, A. angusta*, and *A. rickeri* occur in the Eastern Pacific only (zones 3-9): *Allorchestes carinata*, and *A. bellabella* occur in both the eastern and western North Pacific and overlap throughout the southern Bering Sea and Aleutian Islands (zones 2 & 3). As noted above, the more primitive species occur mainly in the western Pacific region and the more advanced species along North American Pacific shores.

The genus *Parhyalella* is represented on western Pacific shores by *P. kunkeli* and an undescribed species from South Korea (Lazo-Wasem & Gable 2001). *P. pietschmanni* has been fully described from the Hawaiian islands by J. L. Barnard (1970). The reproductive biology of a closely related Malagascan species, *P. steelei*, has been described by Steele (1973). As noted above, *P. barnardi* was initially described from Ensenada, Mexico, leading to speculation that the species may occur also in southern California.

The freshwater genus *Hyalella* is represented by *H. azteca* in streams and lakes throughout the North American coastal region from the tree line of Alaska southward to Mexico (Bousfield 1958; 1996). *H. azteca* is typically dorsally bi-mucronate but a number of genetic species currently being studied by Witt & Hebert (2000), possibly embracing the 4-mucronate variety recorded here from Oregon, may also be present.

TABLE I. CHARACTERS AND CHARACTER STATES: GNATHOPODS

CHARACTER	STATE Plesiomorphic 0	Intermediate 1	Apomorphic 2
Head region			
1. Antenna 1, flagellar length	long (>15 segmts)	13	short (9-11 segs.)
2. Antenna 2, flagellar length	Long		short
3. Maxilla 1, palp	large	small	lacking
Gnathopods (male)			
4. GN1 (male), median spine	horizontal	oblique	vertical
5. GN1, prop palm. p. d. angle	smooth		stout process
6. GN1, prox. palm margin	straight	slightly. convex	convex
7. dactyl unguis	normal		split-tipped
8. dactyl thickness	medially narrowing		medially swollen
9. GN2 propodal palm, ratio P/d	large (>2.6)	medium (2.5)	small (<2.4)
10. carpal lobe, length	short (<		long (>
Gnathopods (female)			
11. GN1, propod depth (L/W ratio)	deep (< 1.8)	medium (1.95)	slender (>2.1)
12. GN2, Propod depth (L/W ratio)	deep (<1.8)	medium (1.9)	slender (>2.0)
13. GN2, palmar slope	oblique	vertical	parachelate
Peraeopods			
14. P4 coxa, lower margin	square		rounded
15. P5, coxa 5 type	posterolobate	aequilobate	sl. anterolobate
16. P 5, segment 4	normal width		broad (W=L)
17. P2, brood plate (female)	large num. setae		small, few setae
Uropods			
18. Uropod 1, peduncular outer marginal spines	uniform along	slight gap	distal gap
19. Uropod 3, Ramus length (ram/ped ratio)	long (>0.8)	medium (0.7)	short (<0.6)
Telson			
20. Depth of apical notch	deep (>1/3)	medium 1/3	shallow (< 1/3)

References:

Austin, W. C. 1985. Amphipoda. **In:** An annotated checklist of marine invertebrates in the cold temperate Northeast Pacific. Khoyatan Marine Lab **3**: 588-623.

Baldinger, A. J., W. D. Shepherd, & D. L. Treloff 2000. Two new species of *Hyalella* (Crustacea: Amphipoda: Hyalellidae) from Death Valley National Park, California, U.S.A. Proc. Biol. Soc. Washington **113** (2): 443-457.

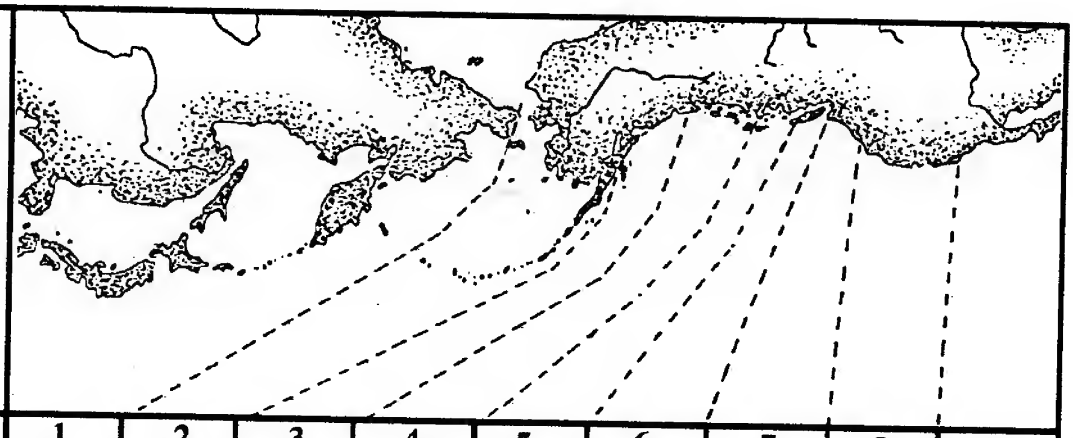
Barnard, J. L. 1952. Some Amphipoda from Central California Wasmann J. Biol. **10** (1): 9-36, 9 pls..

Barnard, J. L. 1954. Marine Amphipoda of Oregon. Oregon State Monogr., Studies Zool. **8**: 9-36, 9pls.

Barnard, 1967. A new genus of galapagan amphipod inhabiting the buccal cavity of the sea turtle *Chelonia mydas*. Proc. Symp. Crustacea at Ernakulum, India **I**: 119-125, 4 figs.

Barnard, J. L. 1969. The families and genera of marine gammaridean Amphipoda. Bull. U. S. Nat'l. Mus. **271**: 1-535, 173 figs.

Barnard. J.L. 1970 Sublittoral Amphipoda (Gammar idea) of the Hawaiian islands. Smiths. Contr. Zool. **34**: 1-286, 180 figs.



DISTRIBUTION ZONES: NORTH PACIFIC RIM									
Hyalellidae: *Allorchestes* sp	1 Western Pacific	2 Bering Sea and Aleut-ians	3 Prince William Sound	4 Cross Sd to Dixon Entrance & Q. C. I.	5 Nor. B. C to North Vanc. I.	6 Central B. C. to S. Vanc. I	7 Washing-ton state	8 Oregon & North Californ	9 Southern Californ
A. malleola	X	?							
A. hirsuta	X								
A carinata	X	X	X						
A. bellabella		X	X	X	X	X	?	x	
A. priceae			?	X	X	X	x	?	
A. angusta		x	X	X	X	X	X	X	?
A. rickeri			x	X	X	X	X	X	?
Hyalella spp.			X	X	X	X	X	X	X
Parhyalella spp	x								x

Fig. 18. Geographical Distribution of North Pacific Genera and Species of Hyalellidae. (X - commonly occurring; x - rare, few records; ? - unrecorded but probable).

Barnard, J. L. 1974. Gammaridean Amphipoda of Australia, Part II. Smiths. Contr. Zool. **139**:1-148 83 figs.

Barnard, J. L. 1975. Amphipoda: Gammaridea. pp. 313-366, pls. 70-85. **In** R. I. Smith & J. T. Carlton (eds). Light's Manual: Intertidal Invertebrates of the Central California Coast, 3rd ed. Univ. California Press: 716 pp..

Barnard, J. L., 1979. Littoral Gammaridean Amphipoda from the Gulf of California and the Galapagos Islands. Smiths. Contr. **271**: 1-149, 74 figs.

Barnard, J. L., & C. M. Barnard, 1883. Freshwater amphipods of the World. Vols. **1** & **2**: 830 pp., 50 figs. 7 graphs, 98 maps, 12 tables. Mt. Vernon, VA. Hayfield Associates.

Barnard, J. L., & G. S. Karaman 1991. The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Part 2. Rec. Australian Mus. Suppl. **13** (Parts 1 & 2): 866 pp., 133 figs.

Bate, C. S. 1862. Catalogue of the specimens of amphipodous Crustacea in the collections of the British Museum, iv + 399 , pls. 1, 1A: 2-58, British Museum Nat. Hist., London.

Borowsky, B. 1984. The use of the males' gnathopods during precopula in some garnmaridean Amphipoda.. Crustaceana **47**(3): 245-250.

Bousfield, E. L., 1958. Ecological Investigations on shore invertebrates of the Pacific coast of Canada. Nat'l Mus. Can. Bull. **147**: 104-115.

Bousfield, E. L., 1963. Investigations on sea-shore invertebrates of the Pacific coast of Canada, 1957 and 1959. I. Station List. Nat'l Mus. Can. Bull. **185**: 72-89.

Bousfield, E. L. 1968. Studies on littoral marine inver tebrates of the Pacific coast of Canada, 1964. I. Station List. Nat'l. Mus. Can. Bull. **223**: 49-57.

Bousfield, E. L. 1981. Evolution in North Pacific Marine Amphipod Crustaceans . in G.G.E. Scudder & J. L. Reveal (eds.), Evolution Today. Proc. 2nd Internat. Congr. Syst. Evol. Biol.: 69-89. 18 figs.

Bousfield, E. L. 1982. Amphipoda: Gammaridea. pp. 254- 285. in Synopsis and Classification of Living Organisms. S. B. Parker (ed.). McGraw-Hill, New York, Vol. 2.: 254-285; 293-294.

Bousfield, 1996. A contribution to the reclassification of Neotropical freshwater hyalellid amphipods (Crustacea: Gammaridea, Talitroidea). Boll. Mus. civ. St. nat. Verona 20: 197-224, 17 figs.

Bousfield, E. L. 2001. Phyletic classification as applied to amphipod crustaceans of North America Amphipacifica 3 (1): 49-119.

Bousfield, E. L. & N. E. Jarrett 1981. Station lists of marine biological expeditions of the National Museum of Natural Sciences in the North American Pacific coastal region, 1966 to 1980. Syllogeus **34**: 1-66.

Bousfield, E. L., & D. E. McAllister 1962. Station list of the National Museum marine biological expedi tion to southeastern Alaska and Prince William Sound. Nat'l Mus. Canada Bull. **183**: 76-103..

Bousfield, E. L, & Shih, C.-t. 1994. The phyletic classification of amphipod crustaceans: problems in resolution. Amphipacifica 1 (3): 76-134.

Bulycheva, A. N. 1957. The sea fleas of the USSR and adjacent waters (Amphipoda: Talitroidea). Keys to the Fauna of the USSR. Acad. Sci. USSR **65**: 1-185, 66 figs. (in Russian).

Chevreux, E. 1902. Campagnes scientifiques de S.A.S. le Prince Albert I de Monaco: description d'un amphipode marin appartenant au genre *Hyalella* Smith. Bull. Soc. Zool. France **27**: 223-227.

Chevreux, E. & L. Fage, 1925. Amphipodes. Faune de France. **9**: 1-488, 438 figs.

Cole, G. A., & R. L. Watkins, 1977. *Hyalella montezuma*, a new species (Crustacea: Amphipoda) from Montezuma Well, Arizona. Hydrobiol. **52**: 175-184, 3 pls.

Dana, J. D. 1849. Synopsis of the genera of Gammaracea. Amer. J. Sci. & Arts. ser 2, **8**: 135-140.

Dana, J. D. 1853. Crustacea. Part II. United States Exploring Expedition **14**: 689-1618, atlas of 96 pls

Dana, J. D. 1856. Catalogue and description of Crustacea collected in California by Dr. John L. LeConte. Proc. Phil Acad. nat. Sci **7**: 175-177.

Della-Valle, A. 1893. Gammarini del Golfo di Napoli. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Monogr. **20**: 948 pp., atlas (61 pls.).

Derzhavin, A. N. 1937. Talitridae of the Soviet coast of the Japan Sea. Issled. Morei SSSR. **23**: 87-112, 6 pl. (Russian with English summary).

Gurjanova, E. F. 1951. Bokoplavy moreii SSSR i sopredel'nykh vod (Amphipoda-Gammaridea). Akad. Nauk SSSR, Opred. po Faune SSSR **41**: 1029 pp., 705 figs.

Hurley, D. E. 1957. Studies on the New Zealand Amphipodan Fauna. No. 14. The genera *Hyale* and *Allorchestes* (Family Talitridae). Trans. Roy. Soc. New Zealand **84** (4): 903-933, 9 figs.

Ishimaru, S. 1994. A catalogue of gammaridean and ingolfiellidean Amphipoda recorded from the vicinity of Japan. Rept. Sado Mar. Biol. Sta. **24**:1-86

Ishimaru, 1995. A new species of the genus *Allorchestes* from floating seaweeds in the Japan Sea. Proc. Japan. Soc. Syst. Zool. 53:48-53, figs.

Iwasa, M. 1939. Japanese Talitridae . J. Fac. Sci. Hokkaido Imp. Univ. ser. 6 Zool. **6**(4): 285-288, 3 figs.

Krapp-Schickel, G., 1974. Camill Hellers Samlung adriatischer Amphipoden - 1866 und Heute. Ann. Naturh. Mus. Wien **78**: 319-379, 28 pls.

Krapp-Schickel, G. 1993. Genus *Parhyalella* Kunkel. in S. Ruffo (ed.). The Amphipoda of the Mediterranean. Part 3. Gammaridea. (Melphidippidae to Talitridae), Ingolfiellidea, Caprellidea. Mem. Inst. Oceanograph. (Monaco) **13:** 577-813.

Kunkel, B. W. 1910. The Amphipoda of Bermuda. Trans. Conn. Acad. Arts & Sci. **16**: 1-116, 43 figs.

Lazo-Wasem, E. & M. Gable 2001. A revision of *Parhyalella* Kunkel (Crustacea: Amphipoda: Gammaridea). Bull. Yale Peabody Museum No **46**:80 pp., 46 figs.

Nagata, K. 1965. Studies on marine gammaridean Amphipoda of the Seto Inland Sea. III. Publ. Seto Mar. Biol. Lab. **13**(4): 291-326.

Ricketts, E. F., & J. Calvin 1968. Between Pacific Tides (4th ed.). Stanford University Press: 614 pp.

Ruffo, S. 1953. Studi sui crostace anfipodi XXXIII. Anfipodi racolte sulle costa del Congo Belga dal Dr. E. Cartevelle. Rev. Zool. Bot. Afr. **47** (1-2): 120-136, 5 figs.

Saussure, H. 1858. Memoires sur divers crustacea nouveaux des Antilles et du Mexique. Mem. Soc. Phys. Hist. Natur. **14P**.2: 417-496, 6 pls.

Schellenberg, A. 1938. Littorale Amphipoden des tropischen Pazifiks. Kungl. Svenska Vetensk. Handl. (3) **16** (6): 105 pp., 48 figs.

Shoemaker, C. R. 1933. Amphipoda from Florida and the West Indies. Amer. Mus. Novit. **598**:1-24, figs.

Smith, S. I. 1874. A synopsis of the higher freshwater Crustacea of the northern United States. Appendix F. Natural History. U. S.Commission of Fish & Fisheries. **2**: 637-661, 3 pls.

Sneath, P. H. A., & R. R. Sokal 1973. Numerical Taxonomy. W. H. Freeman & Co., San Francisco. 573 pp.

Staude, C. P. 1987. Amphipoda Gammaridea. pp. 346-391. **In** Kozloff, A.(ed.). Marine invertebrates of the Pacific Northwest. Univ. Wash. Press: 511 pp.

Stebbing, 1899. Amphipoda from the Copenhagen Museum and other sources. Part II. Trans. Linn. Soc. London (2. Zool) **8**: 395-432 pls. 30-35.

Stebbing, T. R. R. 1906. Amphipoda I. Gammaridea. Das Tierreich: 1-806, figs. 1-127.

Stebbing, T. R. R. 1917. South AfricanTalitridae. Ann. Mag. Nat. Hist. 8: 435.

Steele, D. H., 1973. The biology of *Parhyalella pietschmanni* Schellenberg, 1938 (Amphipoda: Hyalellidae) at Nosy Bé, Madagascar. Crustaceana **25:** 276-280, 4 figs.

Stevenson, M. M., & A. E. Peden, 1973. Description and Ecology of *Hyalella texana* n. sp. (Crustacea: Amphipoda) from the Edwards Plateau of Texas. Amer. Midl. Nat. **89**: 426-436, 7 figs.

Stimpson, W. 1855. Description of some new marine Invertebrata from the Chinese and Japanese Seas. Proc. Acad. nat. Sci. Philadelphia **7**: 375-384.

Stimpson, W. 1857. The Crustacea and Echinodermata of the Pacific shores of North America. J. Boston Soc. Nat. Hist. **6**: 1-92, pls. 18-23

Stout, V. R., 1913. Studies in Laguna Amphipoda. Zool. Jahrb. System. 34: 633-659, 3 figs.

Thomson, G. M. 1880. A new species of Crustacea from New Zealand. Ann. Mag. Nat. Hist., ser. 5, **6**: 1-6, pl. 1.

Tzvetkova, N. L. 1967. K faune ekologii bokoplavov (Amphipoda, Gammaridea) Zaliva Posj'et (Japonskoe More) Akad. Nauk SSSR. Zool. Inst. Issled. Fauny Morei **5**: 160-195, 7 figs.

Tzvetkova, N. L. 1990. An Addition to the fauna of amphipods from the shallow wsaters of East Kamchatka. Proc. Zool. Inst. Leningrad 1990, 218:40-53,10 figs. (in Russian).

Witt, J. D. S,& P. D. N. Hebert 2000. Cryptic species diversity and evolution in the amphipod genus *Hyalella* within central glaciated North America: a molecular phyletic approach. Can. J. Fish. Aquat. Sci. **57**: 687-698.

The Canadian Field-Naturalist: 120 years of northern biodiversity publication

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Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae) in Western North America, with emphasis on species of the *hubbsi* group.

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ABSTRACT

Twenty-eight new species of the Holarctic, freshwater amphipod genus *Stygobromus* are described from a variety of subterranean groundwater habitats in western North America, including caves, springs, wells and the hyporheic zone, and new data are given on species previously described from this region. A total of 53 species are covered in this study, 44 of which are members of the *hubbsi* group. Twenty-three of the newly described species are assigned to this large species group, which is distinguished by the absence of sternal gills (processes). A phylogenetic analysis affirms the monophyly of the *hubbsi* group and suggests that a relatively strong clade of 10 species exists in the far western states of California, Oregon and Washington. A taxon-area cladogram reveals a moderately strong relationship between terminal taxa and physiographic provinces, which are designated as areas in the analysis. In contrast to eastern North America, where many distinct species groups of *Stygobromus* are recognized, taxonomic diversity is significantly reduced among the western species. A majority of species of *Stygobromus* in western North America, especially those in the *hubbsi* group, are closely similar morphologically, leading to the conclusion that many of them are derived from a common ancestor formerly widespread across much of the region.

INTRODUCTION

Species of the large, widely distributed freshwater amphipod genus *Stygobromus* are recorded from a variety of subterranean groundwater habitats, including especially caves, wells, springs and the hyporheic zone beneath surface streams. All members of the genus are stygobites (= stygobionts), inasmuch as they are restricted to subterranean waters (or their resurgence) and are characterized morphologically by loss of eyes and pigment and sometimes by attenuation of the body. *Stygobromus* belongs to the Holarctic amphipod family Crangonyctidae, which contains six extant genera and 152 described species (plus many undescribed). Although members of the family occur in both North America and Eurasia, crangonyctids are far more common and significantly more diverse in North America than in Eurasia. Approximately 80 percent of the species in the family are stygobites, and three of the six genera are exclusively subterranean (Holsinger 1994a).

Prior to publication of the present paper, *Stygobromus* included 101 described species, 98 of which were recorded from subterranean habitats in North America. Outside the continent, two species of *Stygobromus* were reported from central Asia and one from extreme eastern Europe near the Caspian Sea (Holsinger 1987; Kulkina 1992). In this paper, we describe 28 new species from the Cordilleran region of western North America and provide brief synopses for 24 species previously described from this region. We also include *S. putealis* (Holmes) from eastern Wisconsin, which, while occurring far outside the western Cordillera, is morphologically very similar to many species in the west. A majority of species (44 of 53) treated in this paper, including *S. putealis*, are assigned to the *hubbsi* group, which is a large complex of closely similar species erected earlier by Holsinger (1974) to encompass all species in the genus that, with one exception, lack sternal gills (or processes) on the pereonites. A revised diagnosis of the group is given below. The description of 28 new species of *Stygobromus* from western North America, 23 of which are assigned to the *hubbsi* group, brings the total number of described species in the genus to 129. Soon to be added to this total are descriptions of 22 more new species from central and east-central North America that are pending publication in another paper (Holsinger, ms.).

The first comprehensive taxonomic study of western North American species of *Stygobromus* was by Holsinger (1974). In that paper, 17 new species were described from Arizona, California, Orgeon, Montana, Nevada, and Washington and the previously described *S. hubbsi* Shoemaker, 1942 from Malheur Cave in Oregon was partly redescribed. Between 1974 and the present time, six more species were described from western North America. These descriptions included three species from hyporheic habitats and a spring in Colorado by Ward (1977); one species from a cave and one from a spring in the Canadian Rockies of Alberta, respectively, by Holsinger (1980) and Bousfield and

Holsinger (1981); and one species from caves on Vancouver Island, British Columbia by Holsinger and Shaw (1986, 1987). In addition, the monotypic genus *Stygonyx*, a morphologically closely similar sister genus of *Stygobromus*, was described from a phreatic water habitat in northern Oregon by Bousfield and Holsinger (1989). Two undescribed (non-*hubbsi* group) species have also been discovered in Alaska in recent years (see Holsinger et al. 1997) but will be described in another paper.

The principal objectives of the present study are: (a) to describe 28 new species of *Stygobromus* that have been discovered in groundwater habitats of western North America in recent years, primarily during the last two or three decades; (b) update taxonomic and distributional data on previously known species from this region; (c) further clarify the taxonomic and geographic limits of the *hubbsi* group species vis-a-vis other (non-member) species from western North America; (d) conduct a cladistic analysis with the dual purpose of sorting out phylogenetic relationships among western species of *Stygobromus*, especially in the *hubbsi* group, and examining the relationship between phylogeny and geographic distribution; and e) formulate a plausible hypothesis that explains the geographic distribution of numerous, morphologically closely similar stygobitic species over a large part of the highly varied and rugged terrain of the western Cordillera of North America.

We have included distribution maps for all western species of *Stygobromus*, and a table showing the frequency of occurrence of species in different kinds of subterranean groundwater habitats. A phylogenetic analysis was conducted, and the alignment of species in this paper follows the sequence established on the cladogram in which characters are partially weighted and ordered. This cladogram is also converted to a taxon-area cladogram in an attempt to examine the relationship between clades and their geographic distribution. Species assigned to the *hubbsi* group are listed first in the Systematics section, followed at the end of the section by nine non-*hubbsi* group species.

ACKNOWLEDGMENTS

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METHODS AND MATERIALS

Conventional methods for collecting subterranean amphipods have been discussed in previous papers (Holsinger 1967, 1972). Additional comments on collecting methodology as it applies to certain conditions in western North America are found in Ward (1977) and Ward and Holsinger (1981). In the laboratory all measurements were made in millimeters to the nearest tenth with the aid of a calibrated micrometer disc. Total length refers to the length of the body excluding appendages, i.e., length from base of anten-

na 1 to base of telson. The figures were prepared with the aid of a Leitz drawing tube from appendages mounted in Faure's mounting medium (a modification of the conventional Hoyer's medium) on glass slides. Drawings were sometimes made from appendages mounted in undiluted glycerin, in which case these structures were later moved to the more permanent Faure's medium for further clearing and storage. Appendages were not drawn to any particular scale unless noted to the contrary. A legend for figure symbols is provided on page 147.

With the exception of one species, holotype specimens of species described in this paper are deposited in the National Museum of Natural History (Smithsonian Institution) under the catalog numbers of the former United States National Museum (USNM). The exceptional holotype is deposited in the Canadian Museum of Nature collections (CMNC). Collections deposited in other museums are indicated by the museum abbreviation given above under "Acknowledgments". All other specimens examined in this study pertaining to the new species are designated as paratypes and are deposited in the research collection of the second author (JRH) at Old Dominion University. This material will eventually be transferred to the Smithsonian Institution.

In species descriptions, nomenclature for setal patterns on segment 3 of the mandibular palp follows the now widely used standard introduced by Stock (1974) (see Koenemann & Holsinger 2001, fig. 2g, for a recent application). According to this convention, the five different sets of setae that may occur on this segment and are designated by upper case letters A, B, C, D, and E. For the species treated in this paper, as well as most other species of *Stygobromus*, D (row of short setae on inner margin) and E (cluster of longish setae on apex) are the most common and are always present, B and C are less common and often absent, whereas A is almost always absent.

Because vandalism and pollution have become major threats to many cave habitats, we have elected to protect these sensitive environments from further destruction by providing only the name, and a very general location, of caves listed in the "material examined" sections for each species. This protocol applies only to caves, inasmuch as springs, hyporheic habitats, wells, etc. are generally less vulnerable to vandalism or frequent visitation. Thus, if there is legitimate need for a precise cave location, such information can be obtained either from a published state speleological survey (available for some states) or the JRH database upon request. State cave surveys have been published for California (Halliday 1962), Colorado (Parris 1973), and Washington (Halliday 1963). Additional information is available on caves in Oregon (Greeley 1971), and supplementary information on Washington caves was published in the "Guidebook of the 1972 Convention of the National Speleological Society."

SYSTEMATICS

Stygobromus Cope

Stygobromus Cope, 1872:422; *Aprocrangonyx* Stebbing, 1899:422; *Stygonectes* W. P. Hay, 1903: 430; *Synpleonia* Creaser, 1934:1.

Diagnosis. A recent, detailed diagnosis of *Stygobromus* is that of Holsinger (1978). However, the principal diagnostic character of the genus is the uniramous third uropod (U3), in which the ramus is 1-segmented, shorter than the peduncle, sometimes vestigial or absent, and when present armed with 1 to several short spines. The taxonomic and geographic relationship of *Stygobromus* to other genera in the family Crangonyctidae is discussed by Holsinger (1986a, 1986b).

The *hubbsi* group

Diagnosis. Distinguished from all other members of the genus *Stygobromus* (with the exception of one aberrant species in North Carolina) by the absence of sternal gills (processes) on the pereonites and the following combination of characters: mature females larger than mature males; propod of gnathopod 2 usually larger than, but sometimes subequal in size to, propod of gnathopod 1; posterior margin of propod of gnathopod 1 typically shorter than palm, usually without setae but sometimes with few short, submarginal setae just proximal to the defining angle; shape of bases of pereopods 5, 6 and 7 variable but often relatively narrow and not much expanded posteriorly, and often lacking distinct distoposterior lobes; telson usually as long as broad or little longer than broad, apical margin typically with shallow notch.

Stygobromus saltuaris, new species
(Fig. 1)

Material examined. OREGON. Lane Co.: hyporheic/seep area, Trail Creek, Willamette National Forest, HOLOTYPE ♀ (on slide mounts in part) (CMNC 2001-0020), 1 ♀ paratype (CMNC 2001-0021), G. W. Courtney, 25 June 1987.

Diagnosis. A medium-sized hyporheic species, related to *S. oregonensis* in structure of pleonal plates but distinguished by the following: gnathopods 1 and 2 with proportionately longer posterior margin; palm of gnathopod 2 concave; uropod 1 and 2 with fewer long and stout spines on rami and peduncle; uropod 3 peduncle broad; and telson lacking notch and with fewer spines. Largest ♀, 5.0 mm; ♂ unknown.

Female. Antenna 1: 66 percent length of body, 80 percent longer than antenna 2; primary flagellum with 14 segments. Antenna 2: flagellum with 6 segments.

Mandibles subequal: spine row with 4 plumose spines; palp segment 2 with row of 2 rather long setae on inner margin; palp segment 3 bearing 1 B seta, 4-5 C setae, few D setae, and 3 E setae, lacking A setae. Inner lobes of lower lip absent. Maxilla 1: inner plate with 7 apical, plumose setae; palp with 4 stiff setae or slender spines apically. Maxilla 2: inner plate with oblique row of 8 plumose setae on inner margin. Maxilliped: inner plate with 1 bladelike spine, 3 plumose spines, and 3 naked setae apically, and 1 stiff setae on inner margin; outer plate with short setae on inner margin and 1 small bladelike spine on or near apex.

Gnathopod 1: propod shorter than that of gnathopod 2; palm straight or slightly concave about 2 times longer than posterior margin, armed with 13-14 spine teeth in double row; defining angle with 3 spine teeth on outside, 3 shorter ones on inside; posterior margin without setae; 4 superior medial setae; 2 or 3 inferior medial setae; dactyl nail rather long; coxa about as broad as deep, margin with 2 setae. Gnathopod 2: propod subrectangular, 2 times longer than broad; palm slightly concave medially and armed with 13 spine teeth in double row; defining angle with 2 spine teeth of unequal length on outside, 2 shorter spine teeth on inside; posterior margin approximately 70 percent length of palm, with 3-4 sets of doubly inserted setae; 6 superior medial setae, singly inserted; 3 singly inserted inferior medial setae; coxa little broader than deep, margin with 4 setae.

Pereopods 3-4: coxal plates about as deep as broad, margins with 3 setae. Pereopod 6 little longer than pereopod 7, about 55 percent length of body, and 22 percent longer than pereopod 5. Pereopods 5-7: bases of about as broad proximally as distally; posterior margins convex; distoposterior lobes well developed; anterior and posterior margins with variable number of spines and setae; segments 4, 5 and 6 of pereopods 5-7 with longish, slender spines; dactyls of pereopods 5-7 relatively elongate, that of pereopod 6 about 25 percent length of corresponding propod. Coxal gills present on pereopods 2-6, absent from 7. Brood plates slightly expanded distally.

Pleonal plates: posterior margin of plates 1 and 2 slightly concave or nearly straight, with 1 setule near distoposterior corner, that of 3 convex, each with 1 setule near distoposterior corner; distoposterior corners rounded and indistinct; ventral margin of plate 2 with 2 spines, that of plate 3 with 4 spines. Uronites free. Uropod 1: inner ramus little longer than outer ramus, about 80 percent length of peduncle, with 7 spines; outer ramus with 6 spines; peduncle with 6 spines. Uropod 2: inner ramus longer than outer ramus, subequal in length to peduncle, with 7 spines; outer ramus with 4 spines; peduncle with 4 spines. Uropod 3: peduncle usually not bearing small setae; ramus approximately 50 percent length of peduncle, with 3 apical spines.

Telson approximately 30 percent longer than broad, narrowing distally; apical margin with tiny median notch between spine clusters, bearing 10 relatively long spines.

Distribution and ecology. This species is only known from its type-locality, the elevation of which is about 640 m above sea level (G. W. Courtney, pers. comm.). The larger female (5.0 mm) in the series of two has setose brood plates.

Etymology. The epithet *saltuaris* is from the Latin, meaning "forest," in reference to the location of the type-locality in the Williamette National Forest.

Stygobromus rallus, new species
(Figs. 2, 3)

Material examined. WASHINGTON. Whitman Co.: Rock Lake Spring, about 28 km S. of Cheney, HOLOTYPE ♀ (USNM 1000069), 3 ♂♂ and 3 ♀♀ paratypes, 2 juvs., I. Mohammad, 2 July 1992; Spokane Co.: Millers Spring No. 2, 2 ♂♂, 2♀♀, I. Mohammad, 5 Dec. 1992.

Diagnosis. A relatively large groundwater species, closely related to *S. duplus* in gnathopods and uropods 1-2, but distinguished from that species as follows:

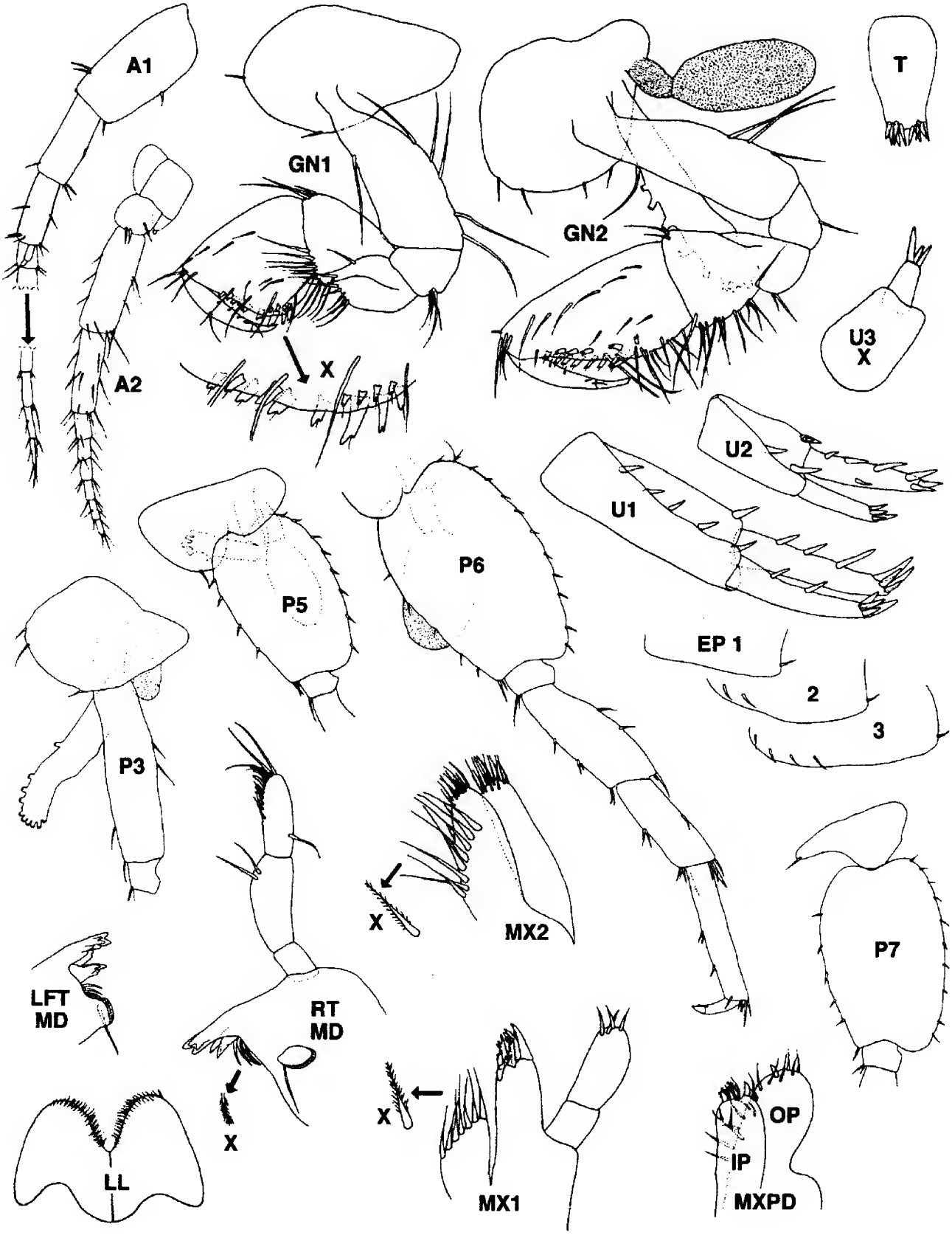

Fig. 1. ***Stygobromus saltuaris*, n. sp.** Female (4.7 mm). Lane County, Oregon.

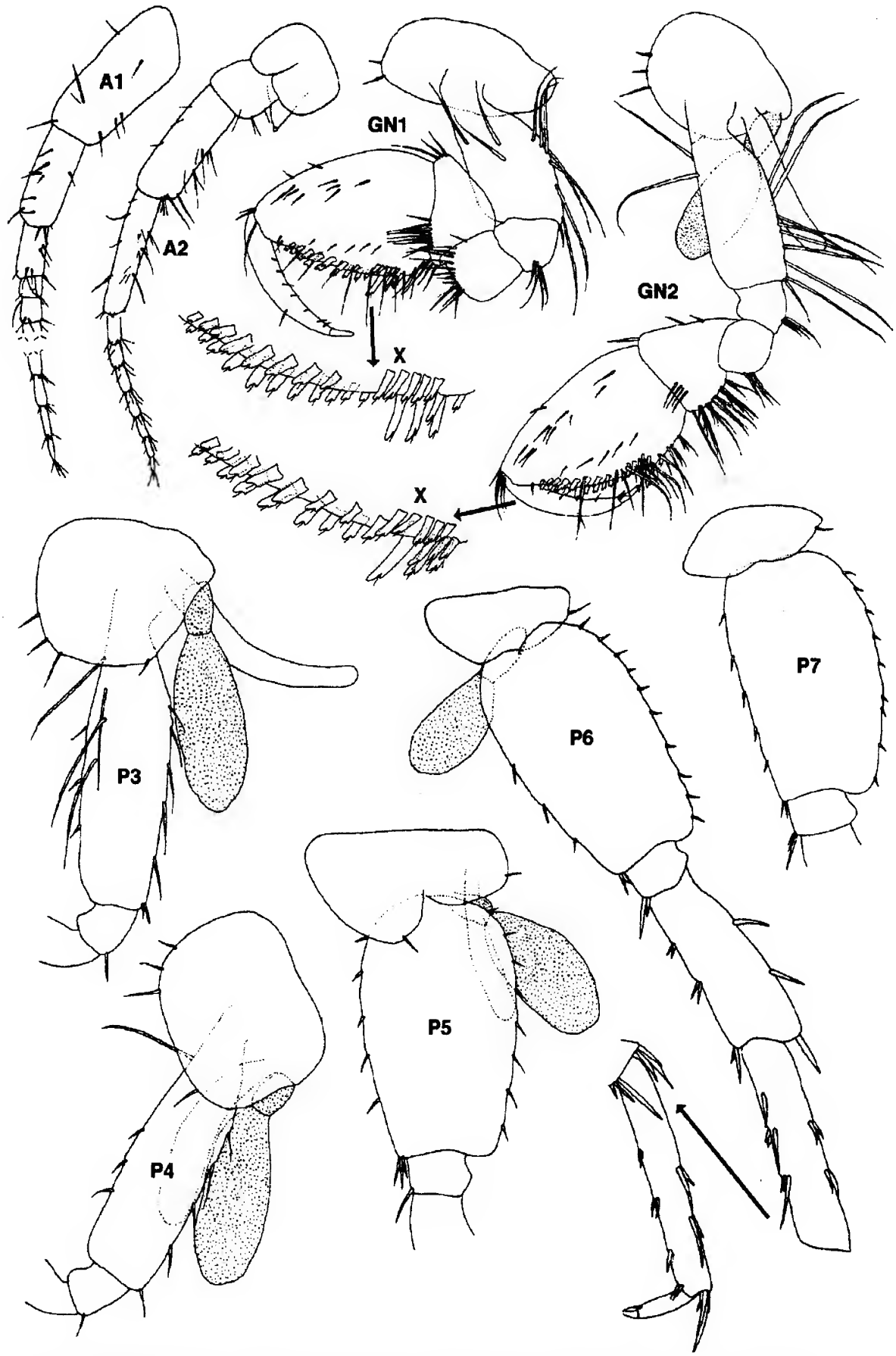

Fig. 2. ***Stygobromus rallus*, n. sp.** Female (7.6 mm). Whitman County, Washington.